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104. Doty, Maxwell S. and Mikihiko Oguri. 1958. Primary productivity patterns in enriched areas. Proc. 9th Pacific Sci. Congress.

111. Banner, Albert H. 1959. Contributions to the knowledge of the Alpheid shrimp of the Pacific Ocean, Part IV. Various small collections from the Central Pacific area, including supplementary notes on Alpheids from Hawaii. Pacific Sci. 13(2):130-155.

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PRIMARY PRODUCTIVITY PATTERNS IN ENRICHED AREAS†

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The variations in oceanic productivity can be thought of as due largely to the interactions of four major factors: phytoplankton, sunlight, inorganic fertilizers, and grazing organisms. The ways these factors are brought together result in primary production, the intensity of which is a function of the changing concentrations of these factors and the inherent abilities of the phytoplankters to produce and reproduce.

While related *(4, 7)*, one must distinguish productivity from standing crop. Productivity is thought of as the actual or potential rate of production. Productivity is generally expressed in terms of mass of material or calories of energy transferred through the particular step under consideration per unit of time per unit of area or volume. Comparable standing crop measurements lack the time element of the productivity measurements. In our primary productivity work the measurements are expressed as the mass of inorganic carbon converted to organic carbon by photosynthesis per unit or time per unit of volume. *A priori* there is little reason why there should exist any particular correlation between productivity and standing crop measurements.

In the ocean, fertilizers are brought into the oceanic euphotic zone from terrestrial, aerial,[1] and dysphotic regions: (a) in transition or shear zones enriched by vertical mixing or eddies, (b) in divergent current areas by upwelling, (c) in wind disturbed areas by the vertical mixing, e.g., in wind cells, and (d) near land by fertilizer increases arising both through concentration by benthic organisms and through addition by freshwater.

The carbon-fourteen technique of determining the primary production rate *(2)* has been applied to the determination of productivity variations in all four such areas. The results are often striking.

As one enters the north subarctic transition zone *(6)* from the south, an increase of about threefold in productivity is found *(3)* (Fig. 1). This appears to be an area enriched by vertical mixing during winter periods, but was formerly considered to be a zone with mixing related to local eddy systems. Sorokin *(8)* reports an even larger similar increase further west. Fig. 1 presents productivity and standing crop data collected during a winter cruise of the U.S. Fish and Wildlife Service vessel, *Charles H. Gilbert*, near 160° W. longitude. It may be seen from this figure that the magnitude of standing crops of zooplankton and phosphate phosphorous is not necessarily directly related to magnitude of productivity, although both may vary in the same direction.

Vertical mixing areas, such as provided by wind cells, can be expected to yield local concentrations, or patches, in which the productivity is significantly greater than that perhaps a hundred meters away. Fig. 2 graphically shows the results obtained from four separate series of samplings across such local areas.

As one approaches land *(1)*, there can be expected to appear in the phytoplankton population, aside from the benthic population, an increase in productivity of at least two orders of magnitude.

When crossing a region of equatorial upwelling, an increase often of nearly one order of magnitude *(5)* can be expected. Fig. 3 reproduced here with the kind permission of the Pacific Oceanic Fishery Investigations of the U.S. Fish and Wildlife Service, shows the productivity of an area of equatorial upwelling in the eastern tropical Pacific. Such has been found correlated with higher concentrations of inorganic fertilizer salts *(5)*; and King *(4)* as well as Murphy and Shomura *(7)*, present figures which provide a picture of the relationships between inorganic physical productivity and certain standing crop factors in the sea.

† This technique was developed with financial assistance provided on contract AT (04-3)-15 with the U.S. Atomic Energy Commission and by funds from the Graduate Research Committee of the University of Hawaii, and on the cruises of Pacific Oceanic Fishery Investigations vessels of the U.S. Fish and Wildlife Service.

[1] Elements added from the air, e.g., nitrogen, are unknown insofar as variations in their rates of addition at sea are concerned.

Contribution No. 104 of the Hawaii Marine Laboratory.

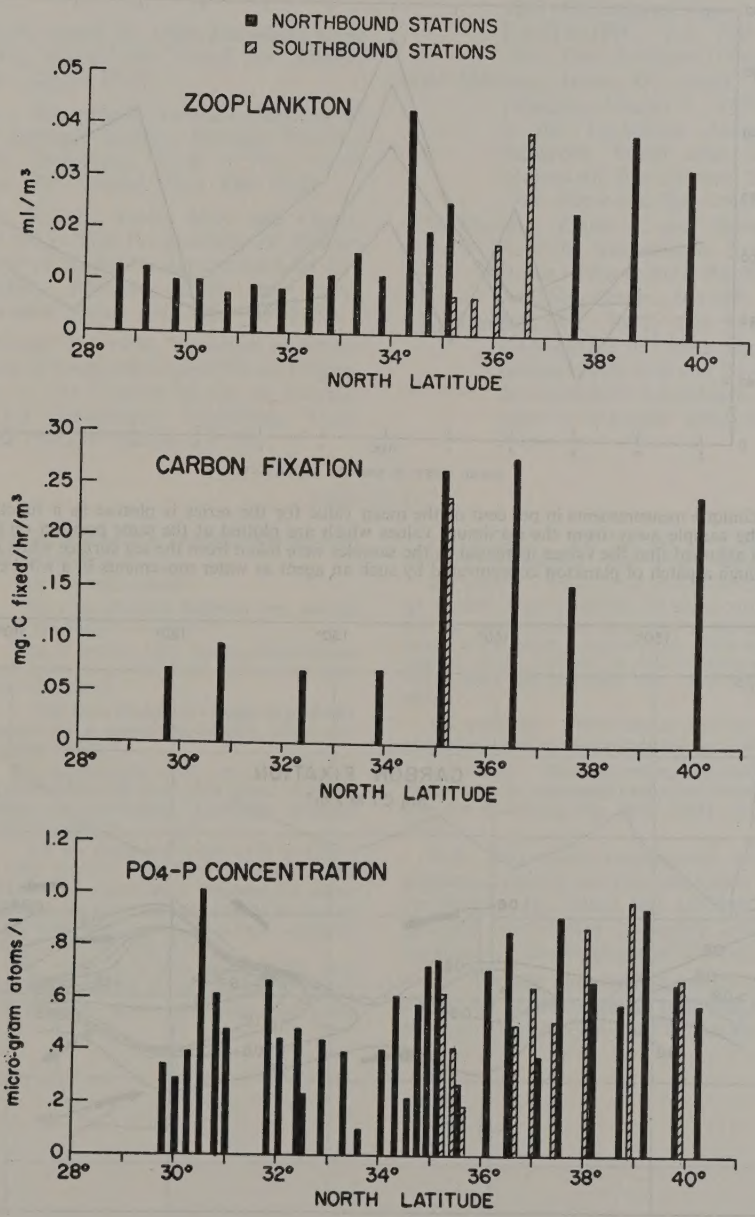

Fig. 1.—Data from Cruise 18 of the U.S. Fish and Wildlife Service vessel, *Charles H. Gilbert*. Productivity and standing crop are plotted as a function of the latitude in the vicinity of 160° W. longitude.

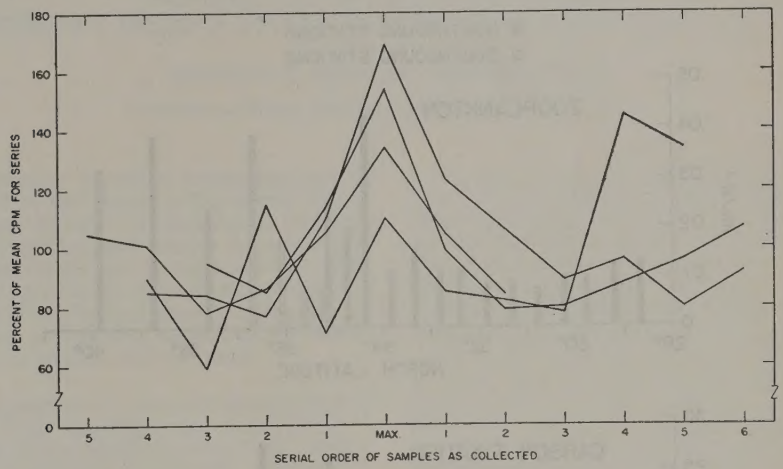

Fig. 2.—C^{14} technique measurements in per cent of the mean value for the series is plotted as a function of the serial order of the sample away from the maximum values which are plotted at the same position on the chart for all series. It is assumed that the values increased as the samples were taken from the sea surface while the vessel drifted slowly through a patch of plankton concentrated by such an agent as water movements in a wind cell.

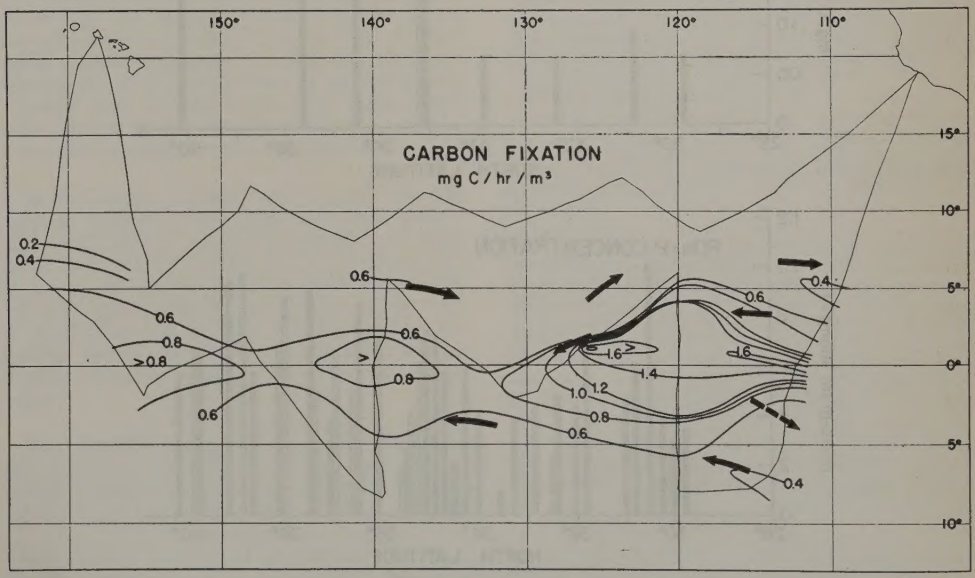

Fig. 3.—Horizontal plot of surface productivity as determined by the C^{14} technique on Crusie 31 of the U.S. Fish and Wildlife Service vessel, *Hugh M. Smith*. The arrows indicate geostrophic currents and are the same as those presented in similar figures in the paper in this symposium by King.

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(7) Murphy, Garth I. and Shomura, Richard S., 1958, Variation in Yellowfin Abundance in the Central Pacific, *Proc. Ninth Pac. Sci. Congr.*, **16**: 108.

(8) Sorokin, J.I., 1957, The Results of Using Radioactive C^{14} for a Study of Organic Matter Cycle in Water Basins, *UNESCO International Conference on Radioisotopes in Scientific Research*, paper 140, 16 pp.

DISCUSSION

J.C. MARR: Is the high peak of production in the wind cells always at their center?

M.S. DOTY: We are not certain.

A.C. HARDY: Was the distance between the patches of phytoplankton production uniform?

M.S. DOTY: This is usually true, but no observations of possible related wind cells were made at the time these particular data were obtained.

T. CROMWELL: We have found no change in quantity of primary productivity approaching islands. Have you ever obtained similar results?

M.S. DOTY: Yes, particularly when very small islands were concerned, but when all such data from our approaches to islands are considered, a reliable increase towards shore seems apparent.

A.C. HARDY: Are the patches circular or in bands?

M.S. DOTY: We assume that they are linear. The results were obtained in experiments designed for other purposes, and the interpretation of the results as due to wind cells is quite hypothetical. No data were obtained which permit a better answer than this.

J.H. RYTHER: In your work near Oahu in the Hawaiian Islands, what is the depth of the thermocline layer?

M.S. DOTY: It is usually below the lowest levels sampled.

J.H. RYTHER: Do you get an actual enrichment as Oahu is approached? How deep is wind mixing?

M.S. DOTY: There is an increase in total phosphorus, as implied from consistent standing crop measurements, but no great increase in inorganic phosphorus has been found as the shore is approached. Wind mixing seemed to extend to the bottom in shallow water near shore and below the 1 per cent light level, at about 100 meters, offshore.

H.S. SWINGLE: Why should you use the productivity of organic carbon, rather than nitrogen, for example?

M.S. DOTY: Because primary productivity of organic carbon can be measured easily and more reliably than is true for measuring any other index of primary productivity.

M.S. Doty also commented on the diurnal rhythm in photosynthetic rate under constant light conditions. He found this rhythm progressively reduced from lower to higher latitudes, related presumably to sharpness of diurnal rhythm.

J.H. Ryther described a recent experiment in which the photosynthetic rate was related to the previous exposure to light or darkness.

Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean
Part IV. Various Small Collections from the Central Pacific Area, including Supplementary Notes on Alpheids from Hawaii

Albert H. Banner

Reprinted from PACIFIC SCIENCE
April, 1959

Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean
Part IV. Various Small Collections from the Central Pacific Area, including Supplementary Notes on Alpheids from Hawaii[1]

Albert H. Banner[2]

In the collections made available to me are a number of small collections, in some cases only single specimens, made from various islands ranging from the Tuamotus to the Carolines, none being extensive enough to warrant separate papers. Some of these have been loaned by the United States National Museum, some by the Bernice P. Bishop Museum, and some by the individual collectors, e. g., the collection by R. W. Hiatt from the islands of Yap. Also, in the continuing collections made in Hawaii since the completion of my 1953 paper, three additional species have been found and two notable variations in the usual form or color of known species have been observed. Finally, a new name has been applied to a species previously described from Hawaii.

Because the specimens came from such widely separated localities and because so few species came from each collection, the collection data are listed under each species rather than in a preliminary comprehensive collection list, as has been done in previous articles.

As in previous papers in this series, instead of repeating the full synonymy for species which have been discussed in previous papers, I have made reference to the earlier papers in the series which have presented the synonymy.

The collections were made for numerous sponsors, some of whom have been forgotten in the many years since the collections were made. This study has been done largely under a grant to the author from the National Science Foundation (NSF G-1754).

Type specimens of the new species described in this paper will be deposited in the institution from which they were borrowed; those types in my personal collection will be deposited either in the Bernice P. Bishop Museum or in the U. S. National Museum (USNM).

Arete Stimpson

Arete dorsalis Stimpson

Arete dorsalis Stimpson, Acad. Nat. Sci. Phila., Proc. 12: 32, 1860.

localities: 1 specimen, Station 1847, Raroia Atoll, Tuamotu Archipelago, "from green-black sea urchin from middle zone of outer reef flats Ngarumaoa Island. . . "; collected by J. E. P. Morrison, July 5, 1952. Four specimens from Station 1857, collection data as above.

discussion: These specimens will be discussed in a future paper dealing with this genus and the genus *Athanas* Leach.

Arete indicus Coutière

Arete dorsalis var. *indicus* Coutière, Soc. Philomath. Paris, Bul. IX, 5(2): 85, figs. 25–30, 1903.

Arete indicus Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2: 863, figs. 134–135, 1905.

[1] Contribution No. 111, Hawaii Marine Laboratory.

[2] Department of Zoology and Entomology, University of Hawaii, Honolulu, Hawaii. Manuscript received February 25, 1957.

TABLE 1
COLLECTION DATA FOR SPECIMENS STUDIED

LOCATION AND COLLECTOR'S NUMBER	ISLAND	ARCHIPELAGO	COLLECTOR	LOANING AGENCY
Tomil Harbor, Nos. Y-111, 122, 214, 215, 252	Yap	Caroline	R. W. Hiatt	R. W. Hiatt
No. 2063	Oneroa	Caroline	Morrison, Doty, Herre	USNM
Kwajalein Atoll	Kwadak	Marshall	P. E. Cloud, Jr.	USNM
Likiep Atoll, No. 827	Nado	Marshall	S. V. MacNeil	USNM
No. 1742	Canton	Phoenix	E. H. Bryan	Bishop Museum
	Jarvis	Line Islands	Toomey, Ahia, Graf	Bishop Museum
	Washington	Line Islands	C. H. Edmondson	Bishop Museum
	Palmyra	Line Islands	C. H. Edmondson	Bishop Museum
No. 3707	Midway	Hawaiian	C. H. Edmondson	Bishop Museum
Nos. 1497, 1498	Wake		C. H. Edmondson	Bishop Museum
	Wake		C. H. Edmondson	Bishop Museum
Pearl and Hermes Reef		Hawaiian	U. S. Navy Ship "Dranga"	Bishop Museum
	Midway	Hawaiian	Y. D. P. Speicer	Bishop Museum
Kaneohe Bay	Oahu	Hawaiian	A. H. Banner	
Ahoolaka, Kaneohe Bay	Oahu	Hawaiian	A. H. Banner	
Wailupe pond	Oahu	Hawaiian	Donald C. G. McKay	Donald C. G. McKay
Raroia Atoll, No. 1847	Ngarumaoa	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2015	Otikaheru	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2187	Kakipuku	Tuomotu	J. P. E. Morrison	USNM
Raroia Atoll, No. 2252	Ngarumaoa	Tuomotu	Maxwell Doty	USNM
Raroia Atoll, No. 1963	Hamahomo	Tuomotu	J. P. E. Morrison	USNM

LOCALITY: 1 specimen, Station 2187, Kakipuku Island, Raroia Atoll, Tuamotu Archipelago, from boring sea urchin; collected by J. E. P. Morrison, August 26, 1952.

DISCUSSION: This specimen, although it lacks all of its appendages, has been put in this species because it compares so well with specimens plainly of this species from the same habitat (holes made by the sea urchin *Echinometra*) collected from Aitutake, Cook Islands. This species will be discussed in a later paper.

SALMONEUS Holthius

Salmoneus tricristata sp. nov.
Fig. 1*a–e*

LOCALITY: 1 specimen, Station Y-122, Tomil Harbor, Yap Island, Caroline Archipelago, an ovigerous female 12 mm. long lacking large chela, having one each of 2nd, 3rd, and 5th legs, and both 4th legs; collected by R. W. Hiatt, 1946.

DESCRIPTION: Rostrum with tip reaching to end of second antennular article, anteriorly narrow but broad at base. Orbital teeth about one-third length of rostrum, tips acute. Both orbital hoods and rostrum bearing dorsal keels, that of the rostrum extending posteriorly from tip to more than two-thirds the length of the carapace, those of the orbital hoods extending almost to the tip of the hood and somewhat shorter than rostral carina.

Antennular articles short and broad. Stylocerite reaching to end of second antennular article. Scaphocerite broad and rounded, lateral spine equal in length to rounded anterior portion.

Large chela lacking. Merus of small chela about 4.5 times as long as broad, broadest in middle; carpus equal in length and breadth to merus, but widest distally; palm a little less than half as long as carpus; fingers equal in length to palm.

First carpal article of second legs slightly longer than the sum of the four distal articles.

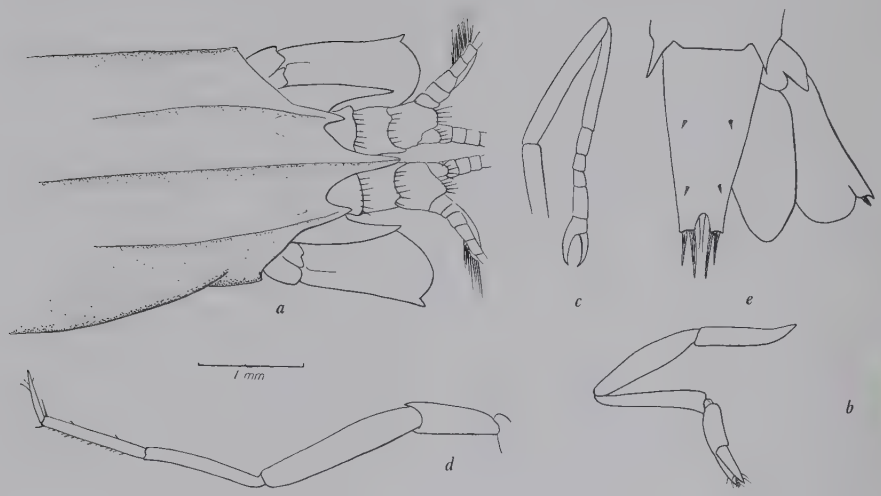

FIG. 1. *Salmoneus tricristata* sp. nov. *a*, Anterior region, dorsal aspect; *b*, small chela; *c*, second leg; *d*, third leg; *e*, telson and uropod. All drawn to same scale.

Third legs with ischium half as long as merus, a little more than twice as long as broad; merus 5 times as long as broad, unarmed; carpus about two-thirds as long and less than half as broad as merus; propodus slightly shorter and thinner than carpus, armed with 4 feeble spines on superior margin and two similar spines on inferior, armed on distal inferior margin with a longer and heavier movable spine; dactylus half as long as propodus, slender, tapering and with a slight curve.

Telson with anterior margin 2.5 breadth of posterior margin and length 4.5 times the posterior breadth; sides with uniform taper; terminal cleft one-ninth length of telson. Tip of telson armed with two pairs of spines, the inner as long as the tip is broad and the outer two-thirds the length of the inner. Cleft bearing two setae. Spines of dorsal surface of telson rather weak.

DISCUSSION: The original name of this genus, *Jousseaumea*, has been changed by Holthius (1955:88) to *Salmoneus*, as the original name was preoccupied.

With Coutière's entirely inadequate description of his three species it is difficult, if not impossible, to be certain of any species. His original description of *Jousseaumea latirostris* (1896:382) was:
"Les épines supra-oculaires sont très peu marquées et le rostre très large. L'une des pattes antérieures manque." In 1897 (p. 234) he added that the large chela was like that of *J. serratidigitus* Coutière, and in 1899 (p. 71, fig. 21) he supplied a dorsal view of the anterior carapace.

As a consequence, until the three species described by Coutière are redescribed adequately, every new species must be regarded as tentative. This species appears to be unique in the possession of the three crests on the anterior half of the carapace. *S. cristata* (Coutière) may have a somewhat similar medial crest, but the two lateral crests represent the continuation of the lateral margins of the rostrum and do not arise from the corneal teeth as do the ones on this species. Other species have the rostral crest, like *S. hilarula* (de Man), but in them it does not extend as

far posteriorly as it does on this species; *S. brevirostris* (Edmondson) has also the crests from the corneal teeth, but again, these do not extend far posteriorly and are not parallel.

If the development of the crests is consistent within a species, and if the interpretation of Coutière's sketches and brief descriptions are correct, this can be regarded as a separate species.

SYNALPHEUS Bate

Synalpheus coutierei Banner

Synalpheus biunguiculatus Coutière (*nec* Stimpson), Soc. Ent. de France, Bul. (11): 232, figs. 1–4, 1898.

Synalpheus coutierei Banner, Pacific Sci. 7(1): 36, 1953.

LOCALITY: 1 specimen, Bernice P. Bishop Museum No. 1742, Canton Island, Phoenix Archipelago; collected by E. H. Bryan, 1924.

DISCUSSION: While this specimen is definitely *S. coutierei*, it differs slightly in the rostrum and antennular peduncle from the illustration of Coutière. In his figures the orbital hoods are thinner than those in this specimen (which even exceeds the breadth as shown for *S. pachymeris*, *loc. cit.*, fig. 9) and the rostrum is definitely shorter than the orbital teeth and relatively thinner. In the antennular peduncle the articles are thinner and longer, but not markedly so, while the relative proportions of the parts of the antennular peduncle remain about the same. Considering the variation in the genus and the variation already reported for *S. coutierei*, this is probably not important.

Synalpheus carinatus (de Man)

Alpheus carinatus de Man, Arch. f. Naturgesch., 53: 508, pl. 22, fig. 2, 1887.

LOCALITY: 4 specimens, Kwadak, Kwajalein Atoll, Marshall Islands, from specimens of *Comanthus bennetti* (Müller) as determined by A. H. Clark, U. S. National Museum; collected by P. E. Cloud, Jr.

Synalpheus charon obscurus Banner

For synonymy, see Banner, Pacific Sci. 10(3): 329, 1956.

LOCALITIES: 1 specimen, Bishop Museum No. 3707, from Midway Island, Hawaiian Archipelago; 1 specimen, Bishop Museum No. 1497, from Wake Island (19°18′ N., 166° 35′E.), in coral; both collected by C. H. Edmondson, Tanager Expedition, 1923.

DISCUSSION: These specimens plainly belong to the new subspecies; the specimen from Midway, an ovigerous female, is 20 mm. long, the largest specimen yet seen.

Synalpheus paraneomeris Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 331, 1956.

LOCALITIES: 2 specimens at Station 287, USNM 194726, from Likiep Atoll, Nado Island, Marshall Islands; collected by S. V. MacNeil. Two specimens from Jarvis Island, Line Islands; collected by Toomey, Ahia, and Graf, Itaska Expedition, 1935. One specimen from Wake Island; collected by C. H. Edmondson, Tanager Expedition, 1923.

DISCUSSION: The large chela of the male specimen from Wake Island has a ratio of the chela length to the finger length of 2.6, the longest finger yet encountered (see Banner, *loc. cit.*). The specimen otherwise agrees with the variable characteristics of this species.

Synalpheus tuthilli sp. nov.
Fig. 2*a–j*

TYPE SPECIMEN: An ovigerous female 12.6 mm. long, Station Y-215, Tomil Harbor, Yap Island, Caroline Archipelago; collected by R. W. Hiatt, 1946. An allotype, 10.5 mm. long, and 7 paratypes from same station.

DESCRIPTION: Rostrum short, reaching less than one-third the length of the visible portion of first antennular article; sides straight, with uniform taper, orbital teeth short, slightly shorter than rostrum, tips rounded, both medial and lateral margins slightly concave.

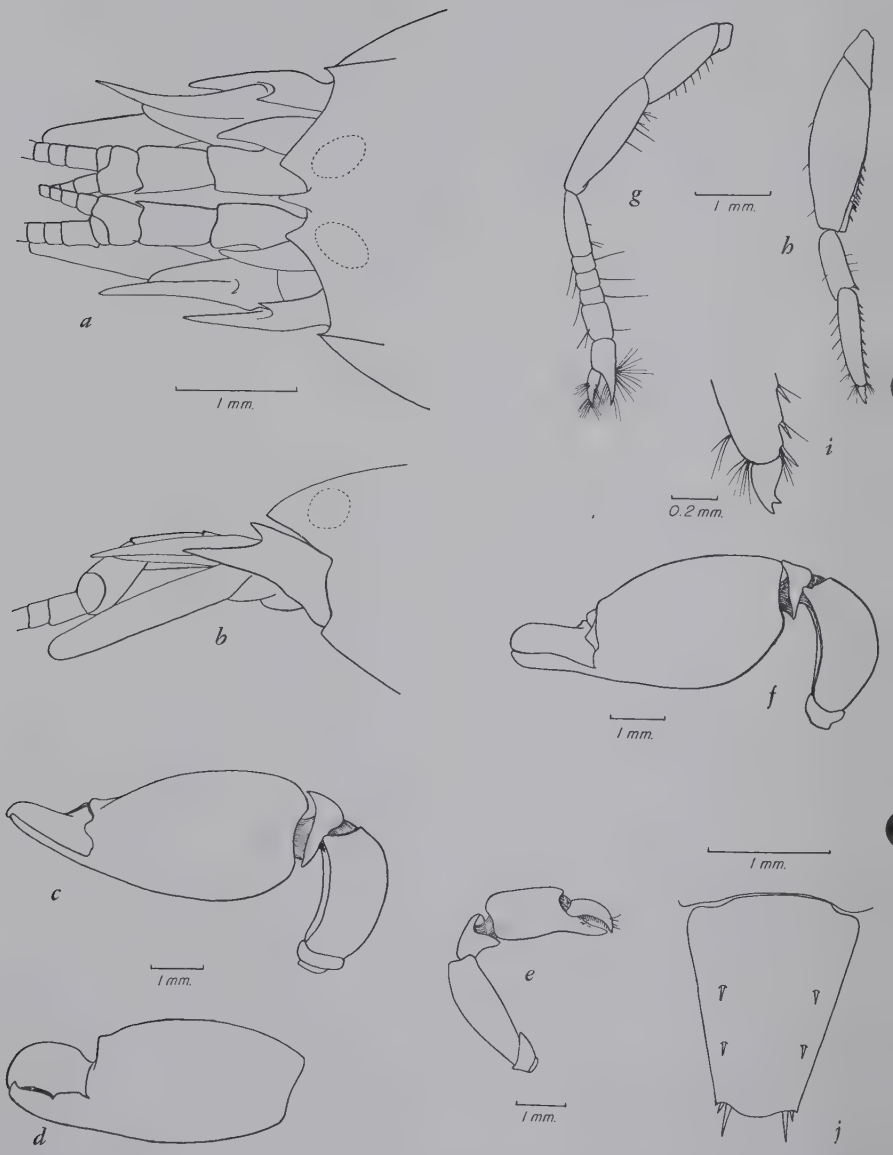

FIG. 2. *Synalpheus tuthilli* sp. nov. *a*, *b*, Anterior region, dorsal and lateral aspects (assymetry of scaphocerites are as found in specimen); *c*, large cheliped, female, lateral aspect; *d*, same, superior face; *e*, small cheliped, female; *f*, large cheliped, male; *g*, second leg; *h*, third leg; *i*, third leg, dactylus; *j*, telson.

Orbital hoods and rostrum depressed and rounded in lateral view.

Antennular peduncle with first article slightly longer than second; second article about twice length of third article. Stylocerites heavy, with slightly rounded tips not reaching to end of first antennular article. Lateral spine of basicerite reaching almost to middle of second antennular article. Stylocerite with lateral spine well developed (that of right side distorted on type specimen), reaching to end of antennular peduncle; blade reduced, narrow and reaching only to end of second antennular article. Carpocerite markedly longer than antennular peduncle.

Large chela inflated, subcylindrical in section, 2.4 times as long as broad, tapering strongly to fingers. End of palm above dactylar articulation unmarked by any prominences. Fingers occupying distal quarter of entire length of chela, twisted from axis of palm; dactylus high, narrow, with superior edge rounded. Merus short, less than half length of chela, heavy, twice as long as broad, and strongly curved, with superior margin more strongly curved than inferior; superior margin not terminated in angle, but curved towards dactylar articulation.

Small chela small but heavy, with palm 1.6 times as long as broad, and 1.7 times as long as fingers; fingers tapering, slightly broadened proximally. Merus about as long as that of large cheliped, almost as long as small chela proper; superior margin curved but not as strongly as that of large cheliped; inferior margin straight.

Carpal articles of second leg with ratio: 10:2.5:2.5:2.5:6.

Third legs with merus heavy, three times as long as broad, with inferior distal margin bearing numerous short spines which are usually concealed in normal side view by larger outer (or posterior) ridge. Carpus as long as merus is broad, superior margin ending in rounded tooth, inferior margin terminally armed with single weak spine. Propodus 0.56 as long as merus, 4.5 times as long as broad, armed with 9 weak spines. Dactylus less than 0.2 length of propodus, with strong taper and small ungui.

Telson 2.7 times as long as broad at posterior margin, with anterior margin twice as broad as posterior; lateral margins slightly convex in middle, terminated by slight subacute angles; posterior margin with low convexity.

DISCUSSION: In the nine specimens in the collection little variation is present except for the large chela and the armature of the merus of the third legs. In the larger specimens the length of the finger in respect to the chela is like that of the type, but in some of the smaller specimens the fingers occupy up to 0.32 the length of the chela; the fingers of the small specimens are also more slender, being as much as 2.6 times as long as broad. It should also be noted that the merus of the allotype is more strongly curved than that of the type. The merus of the third legs bears from 3 to 9 spinules, with the small number being on the smaller specimens.

It is also interesting that of this small collection, two males and one female (ovigerous) bear parasitic isopods on their abdomens.

This form is plainly related to *S. pachymeris* Coutière (1905*a*: 873) and *S. bituberculatus* de Man (1910: 294), and less closely to *S. coutierei* Banner (1953: 36) of the Coutierei group (see description under the name *S. biunguiculatus* (Stimpson) in Coutière, 1898: 230). The last species differs from the first two and from this form in that the merus of the third legs is unarmed. This form differs from the first two species in that the margin of the palm above the dactylar articulation is unarmed and the palm itself is inflated, while in both others the palm is more slender and bears one (*S. pachymeris*) or two (*S. bituberculatus*) rounded projections above the dactylus. There are also slight differences in the armature of the anterior carapace, but it is unlikely that these are of significance. In *S. pachymeris* and *S. bituberculatus* (but not in *S. pachymeris cargadosi* Coutière) the stylocerites are longer than the

first antennular article, but they are shorter in this form. Coutière regarded the number of spinules on the merus of the third legs as important in his description of his variety *S. p. cargadosi* (1921: 417), but neither in de Man's species, nor in Coutière's original description (where he described *pachymeris* as a variety of *S. biunguiculatus*=*S. coutierei*), any more than in these specimens, were the number of spinules constant between individuals.

Unfortunately the name *tuthilli* used in the genus *Alpheus* will have to be put in synonymy in a subsequent paper; this is another attempt to express thanks to Dr. Leonard D. Tuthill, friend and former editor of *Pacific Science*, for the help he has given me.

ALPHEUS Fabricius

Megacheles Group

Alpheus lanceostylus sp. nov.
Fig. 3*a–b*

Alpheus species 1, Banner, Pacific Sci., 10(3): 338, 1956.

TYPE: 28 mm. male collected at Pearl and Hermes Reef, Hawaiian Archipelago (27°N., 146°W.), by U. S. Navy Ship "Dranga" in 1927. Bernice P. Bishop Museum No. 2737.

PARATYPE: An ovigerous female 22 mm. long without chela collected from Saipan, Marianas (probably from the reef flat west of Cape Nafutan—exact data are lost), by A. H. Banner in 1945.

DESCRIPTION: Rostrum acute, reaching beyond end of first antennular article, broad at the base, dorsally only slightly rounded. Orbitorostral borders slightly concave. Orbital teeth strong, similar in shape to rostrum and about half as long.

Antennular peduncle with the second article 1.6 times the length of the visible portion of the first article, 1.2 times the length of the second article, and 1.3 times as long as broad. Stylocerite acute and reaching to middle of second antennular article. Scaphocerite broken on right side, left side with broad squamous portion reaching almost to tip, and tip slightly exceeding end of third antennular article. Carpocerite reaching slightly beyond end of scaphocerite. Lateral spine of basicerite not heavy, and reaching to level of tip of rostrum.

Merus of large cheliped with inner face 1.5 times as long as maximum breadth distally; superior margin terminating in subacute tooth; inferior external margin irregular but not bearing spines; inferior internal margin bearing 10 small movable spines and terminating distally in strong acute tooth. Ischium bearing 4 inferior spines and a strong superior tooth. Carpus bearing a rounded tooth on superior internal distal margin. Chela heavy, compressed, almost as broad distally through the fingers as proximally, 2.9 times as long as broad. Superior crest of palm terminating distally in strong acute tooth, interrupted by shallow and poorly defined transverse groove, and proximally merging with surface of chela. Superior groove shallow and flattened. Palmar crest broadly rounded and poorly defined proximal to transverse groove. Palmar groove broad and rounded. Inferior crest distinct only distally and ending in strong tooth. Inferior depression deep but rounded. Shoulder distinct but not abrupt. (For explanation of terms see Banner, 1953, fig. 17e). Fixed finger strongly curved. Dactylus closing across end of chela, thin with high sharp crest, and strongly curved; superior margin without marked lobes, inferior margin with what appears to be an extra rounded tooth. Cheliped bearing only scanty setae except near fingers where setae are somewhat heavier.

Small chela lacking in both type and paratype.

Carpal article of second legs with ratio 10:7:4:3:5.

Third legs with ischium bearing movable spine; merus 6.6 times as long as broad, unarmed; carpus unarmed and 0.5 length of merus; propodus bearing 7 weak spines, 0.7 as long as merus; dactylus slender, curved, with single superior serration.

Telson 1.4 times as broad proximally as distally, 2.5 times as long as tip is broad, with

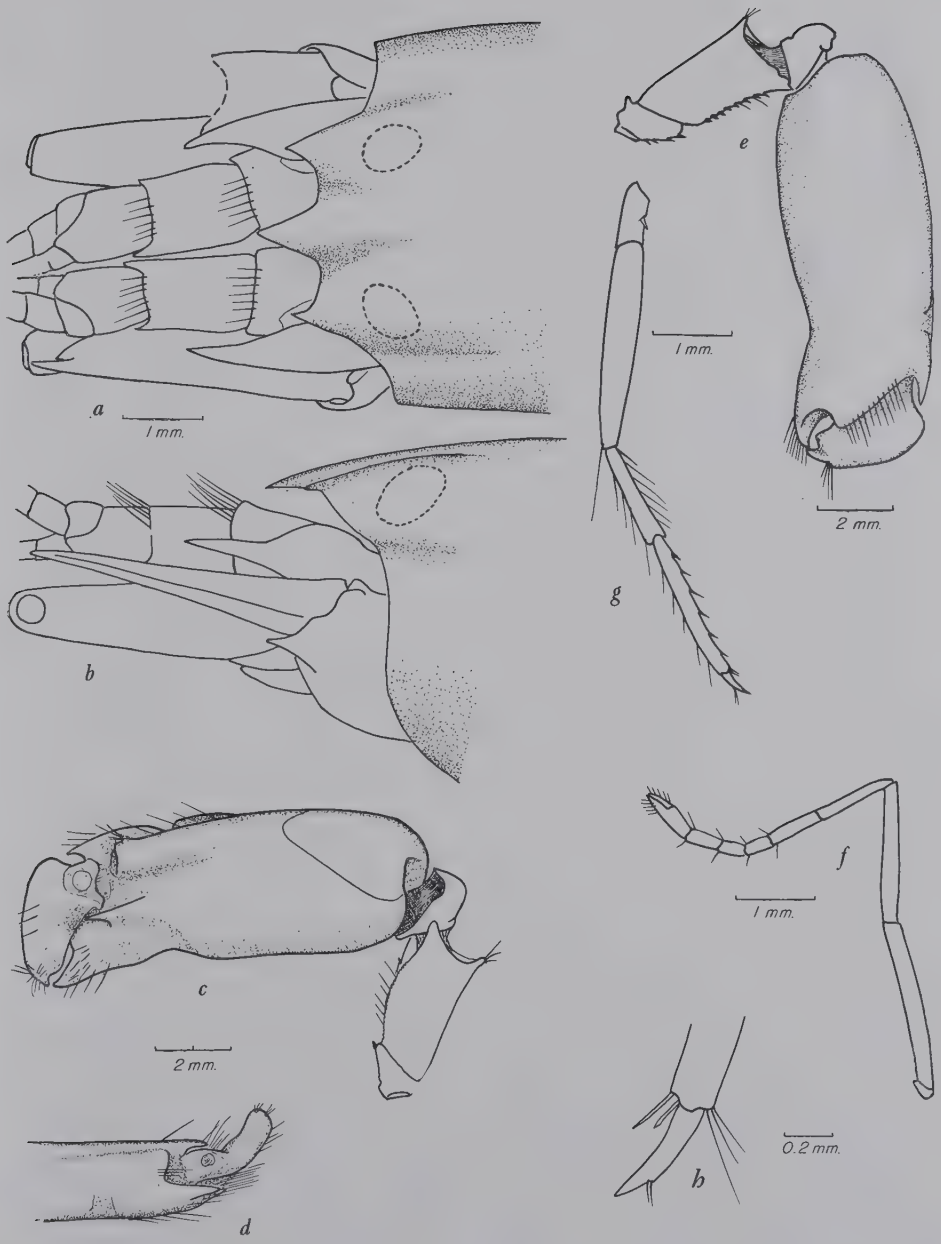

FIG. 3. *Alpheus lanceostylus* sp. nov. *a*, *b*, Anterior region, dorsal and lateral aspect; *c*, *d*, large cheliped, lateral and medial aspect; *e*, large chela, tip, superior aspect; *f*, second legs; *g*, third legs; *h*, third leg, dactylus.

lateral margins almost straight. Anterior dorsal spinules 0.3, posterior 0.6, of the length from articulation to tip.

DISCUSSION: The only difference noted between the incomplete specimen from Saipan and the type is that the propodus of the third legs carries 9 instead of 7 spines.

This species plainly belongs to the Megacheles group, and to the *A. hailstonei* Coutière complex (see Banner, 1953, p. 51 *et seq.*). However, it can be sharply separated from all others of that group (including *A. staphylinus* Coutière) by a series of characters, which include the broad second article of the antennular peduncle, the long stylocerite, and the nature of and direction of closure of the dactylus of the large cheliped. Other characteristics will separate it from one or more of the complex, as the presence of ischial spines will separate it from *A. hailstonei hailstonei* Coutière and *A. brachymerus* (Banner); the armature of the dactylus from several others, etc. (*op. cit.*, p. 55).

It is difficult to state which of the known species of the complex is most closely related to the new species. On the basis of the anterior carapace, large chela, and third leg it appears to be closest to *A. hailstonei paucispinata* (Banner).

Alpheus collumianus medius Banner

For synonymy, see Banner, Pacific Sci. 10(3): 340, 1956.

LOCALITIES: 2 specimens, Station Y-215, Tomil Harbor, Caroline Archipelago; collected by R. W. Hiatt. One specimen, Jarvis Island, Line Islands, Itaska Expedition; collected by Toomey, Ahia, and Graf, 1935. One specimen, Wake Island (19°18′N., 166° 35′E.), collected by C. H. Edmondsom, Tanager Expedition, 1923.

DISCUSSION: Of the two specimens from Tomil Harbor, Yap, one was similar to the type in all respects, but the other, also similar, showed assymetry in the basicerites, with one normal for the subspecies and the other like that of *A. c. inermis* Banner (1956:342).

The one specimen from Midway was also very similar to the type specimens except that its only remaining second leg had the carpus divided into six rather than five articles. The ratio of these articles was 10:2:9:4:4:7, showing that the extra article was the short one between the first and second articles.

Alpheus seurati Coutière
Fig. 4

Alpheus seurati Coutière, Fauna and Geog. Maldive and Laccadive Archipelagoes 2(4): 881, pl. 75, fig. 20, 1905.

LOCALITY: 1 specimen from Jarvis Island, Line Islands; collected by Toomey, Ahia, and Graf, Itasca Expedition, 1935.

DISCUSSION: This sole specimen of the species agrees almost perfectly with the description and figures of Coutière, although it lacks the small chela.

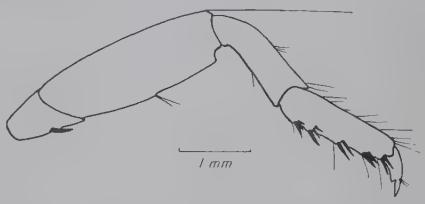

FIG. 4. *Alpheus seurati* Coutière. Third leg.

This species is plainly most closely related to *A. collumianus* Stimpson and within *A. collumianus* to the two subspecies, *A. c. medius* and *A. c. inermis* Banner (1956: 340). Coutière points out that the form of the anterior carapace, the large chela, the second legs, and the telson are like *A. collumianus* (actually, more like *A. c. medius*); the differences lie in the stylocerite—which is like that of *A. c. inermis* —and in the third legs, where the merus is broadened and lacking an acute distal tooth, but bears rather a rounded protuberance. He also points out several other characteristics that differ, but these, like the relative lengths of the second legs and the presence or absence of spines on the carpus of the third legs, are

variable characteristics, at least between the present subspecies.

I believe, therefore, that if the two subspecies are acceptable this species, too, should be made a subspecies of *A. collumianus;* however, I have deferred the action until more specimens can be examined.

Macrochirus Group

Alpheus huikau nom. nov.
Fig. 5*a–e*

Crangon nanus Banner, Pacific Sci. 7(1): 90, figs. 30, 31, 1953.

Alpheus nanus Banner, Pacific Sci. 10(3): 345, 1956.

nec Crangon nanus Krøyer, Naturhist. Tidsskr. 4(3): 231, 1842.

LOCALITIES: 13 specimens, Station 827, USNM 194726, Nado Island, Likiep Atoll, Marshall Islands; collected by S. V. MacNeil, 1952. One specimen, Station 2252, Ngarumaoa Island, Raroia Atoll, Tuamotu Archipelago; collected by Maxwell Doty, Sept. 3, 1952.

DISCUSSION: It has been necessary to apply a new name to this species, which was named when the genus was called *Crangon* instead of *Alpheus*, because of Krøyer's use of *Crangon nanus* in 1842 for a species no longer in *Crangon* (or *Crago*) in 1953. The new name is from the Hawaiian, and means "confusion" or "mixed-up mess."

This group of specimens presents three points worthy of discussion. First, while the chelae on all of the females are like those described from Hawaii, the three males in the collection, all between 10 and 11.5 mm. in length, present an overgrowth of the fingers of the large and small chelae similar to that reported below for *A. paragracilis* Coutière. In the large chela the dactylus is very elongate, acute, and curved; the fingers occupy a large proportion of the length of the chela. The inferior internal margin of the merus only bears two feeble spinules, fewer than those reported in specimens in the Marianas and

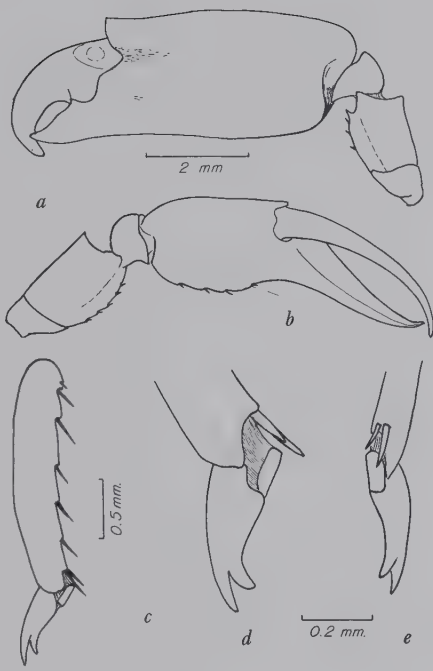

FIG. 5. *Alpheus huikau* nom. nov. *a*, *b*, Large and small chelipeds, showing overgrowth of fingers; *c*, third leg, merus and dactylus, anterior or medial aspect; *d*, *e*, third leg, dactylus, posterior and inferior aspects.

Arno. The small chela of the males also has the fingers elongate and curved; the merus is armed with two strong spines and three weaker spinules; the inferior margin of the palm bears two strong spines and two weaker spines, a characteristic not observed in previous specimens. This development of the chelae in the largest specimens is similar to that found for *A. paragracilis*. Unfortunately, neither this series of specimens, nor those from other islands, present a picture of gradual development as is found for *A. paragracilis;* however, a few other larger males, like those from Arno, do have a tendency towards the longer dactyli.

Second, is the peculiar development of an extra chitinized piece proximal to the dactylus and inferior to the distal end of the merus of

the third to fifth legs. This piece is borne by the tendon that reaches to the "heel" of the dactylus and is ordinarily obscured by the spines at the end of the dactylus if the animal dies with the dactyl straight or flexed towards the propodus. In many of these specimens, however, the dactylus was bent back on the propodus in death, so that the extra plate is apparent. The extra piece fits into an emargination of the inferior distal end of the propodus when the dactylus is straight or flexed. Other specimens of this species were re-examined and it was found that this development was carried by specimens from all areas studied. Moreover, specimens of the closely related *A. paragracilis* were also found to have the same structure.

Third, the outer uropods of these specimens bear several broad teeth on the distal articulation, and the inner uropod on its outer distal margin bears several small spines; neither of these characteristics was found in the specimens from Hawaii. This difference is not considered worthy of taxonomic emphasis.

The single specimen from the Tuamotus differs from the Hawaiian specimens in two minor ways. First, the rostrum is slightly shorter instead of slightly longer than the orbital hoods; second, the third and fourth carpal articles of the second legs are 1.3 and 2.0 times as long as broad instead of being broader than long. This latter characteristic may be important, but one specimen is not adequate for drawing such a conclusion.

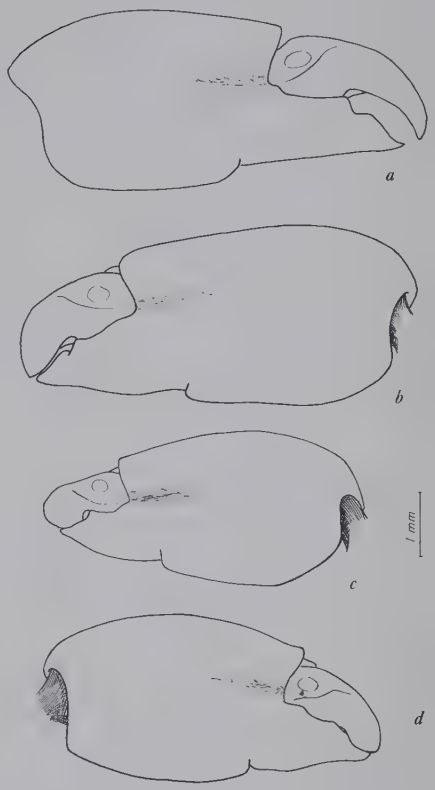

FIG. 6. *Alpheus paragracilis* Coutière, variation in the large chela. *a*, Male, 11.4 mm. long; *b*, male 10.8 mm. long; *c*, female, 11.4 mm. long; *d*, male, 9.6 mm. long. All drawn to the same scale.

Alpheus paragracilis Coutière
Fig. 6*a–d*

For synonymy, see Banner, Pacific Sci. 10(3): 345, 1956.

LOCALITIES: 1 specimen, Station Y-252, Yap Island, Caroline Archipelago, under small rocks on outer reef; collected by R. W. Hiatt, 1946. Nine specimens, Midway Island, Hawaiian Archipelago; collected by Y. Speicer, 1941.

DISCUSSION: These specimens present an interesting series on the change of form of the large chela with growth. The smaller males, less than 9.0 mm. long, and the females of all sizes have similar chelae, about twice as long as broad, and about 3.5 times the length of the fingers; the fingers of the dactylus are short, heavy, and rounded distally. However, on the largest male in the collection, 11.4 mm. long, the chela is 2.4 times as long as broad, and only 2.3 times the length of the fingers, and the dactylus is long, thin, curved and acute on the end. Between these two condi-

tions are found intermediate males, progressing from rounded condition of the immature forms to the acute form of the oldest male. It is also noteworthy that the chelae in the males are 1.5 times the length of those of the females of the same size.

In other collections examined and reported upon in previous papers, including those from Hawaii, this condition was not seen.

Alpheus macrochirus Richters

For synonymy, see Banner, Pacific Sci. 11(2): 198, 1957.

LOCALITIES: 2 specimens, Washington Island, Line Islands, in coral, Whippoorwill Expedition; collected by C. H. Edmondson, August, 1924.

Alpheus edmondsoni (Banner)

Crangon edmondsoni Banner, Pacific Sci. 7(1): 78, fig. 26, 1953.

LOCALITY: 1 specimen, Station 2063, Oneroa Island, Caroline Archipelago, from surge channel, on outer reef beyond *Lithothanmion* ridge; collected by Morris, Doty, and Herre, August 6, 1952. (Specimen without chelae, therefore identification questionable.)

Alpheus ventrosus Milne-Edwards

For synonymy, see Banner, Pacific Sci. 10(3): 345, 1956.

LOCALITIES: 2 specimens, Station Y-214, Tomil Harbor, Yap Island, Caroline Archipelago, in *Pocillopora* at 3.0 feet; collected by R. W. Hiatt, 1946. Eight specimens from racimose coral heads east side Tomil Harbor, Station Y-215; other data as above. Two specimens from Kaneohe Bay, Oahu, Hawaiian Archipelago; collected by A. H. Banner, August 24, 1955.

DISCUSSION: The pair of specimens, male and female, from Hawaii are included in this paper because of their unusual color pattern. Wherever I have collected this species in the Pacific the color has been the same, a basic orange red, with spots and sometimes stripes of deeper red. This pair, from the same head of *Pocillopora meandrina* var. *nobilis* Verrill, had in life a ground color of white with a tinge of pinkish yellow, and carried a series of paired irregular dark reddish-brown spots on either side of the middorsal line, three pairs on the carapace, and one pair on each abdominal somite. Similar but smaller spots were found at the bases of the abdominal pleura. Only the large and small chelae had the color usually characteristic of this species. The female carried larvae, recently hatched but still clinging to the pleopods, of pale violet color. No morphological differences were found between these and the normally colored specimens.

Obesomanus Group

Alpheus lutini Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 346, 1956.

LOCALITIES: 1 specimen at Y-214, 2 at Y-215, collection data as in *A. ventrosus* above.

Alpheus phyrgianus Coutière

For synonymy, see Banner, Pacific Sci. 10(3): 346, 1956.

LOCALITY: 1 specimen from Palmyra Island, Line Islands, in coral; collected by C. H. Edmondson on Whippoorwill *A* Expedition, August, 1924.

Crinitus Group

Alpheus frontalis H. Milne-Edwards

For synonymy, see Banner, Pacific Sci. 10(3): 357, 1956.

LOCALITY: 2 specimens, Station 1963 from Hamahomo Island, Tuamotu Archipelago, in algal tubes, under rocks, near shore; collected by J. E. P. Morrison, July 21, 1952.

Diadema Group

Alpheus diadema Dana

Fig. 7*a–e*

For synonymy, see Banner, Pacific Sci. 10(3): 357, 1956.

LOCALITIES: 2 specimens, Midway Island, Hawaiian Archipelago; collected by Y. D. P. Speicer, 1941. Six specimens, Ahoolaka ("Sand Island"), Kaneohe Bay, Oahu, Hawaiian Archipelago, under coral heads; collected by A. H. Banner, August, 1955.

DISCUSSION: In the group of specimens from Kaneohe Bay listed above an interesting variation occurs in the dactyli of the third, and to a lesser extent, the fourth legs. In most of the specimens from Hawaii these dactyli are either simple like the neotype (Banner, 1953, fig. 43j) or with a very small thickening or shoulder similar to those shown in Figure 7*c*, *d*. However, in this group of specimens from Kaneohe Bay, three specimens, male and female, have a definite and well-developed secondary unguis (Fig. 7*a*); the other specimens from the same locality had the secondary unguis developed as a shoulder only (Fig. 7*b*). There are no other noteworthy variations in either group of specimens. In the whole series of specimens it is the third legs that have the greatest development of the secondary unguis, and usually the fourth have but a slight thickening at most; moreover, often the accessory tooth or shoulder is not of uniform bilateral development.

The extensive collections of this species from the central Pacific area were spot checked for this characteristic, and it was found that most specimens were of intermediate development, similar to the conditions shown in Figure 7*b–d*. The extreme development, similar to the conditions shown in Figure 7*a* and *e*, were both rare.

Obviously, no significance should be attached to this variation.

An error in the redescription (Banner, 1953: 119) should be corrected. In describing the dactylus of the third legs, the text states: "Dactylus simple . . . as long as merus." In-

FIG. 7. *Alpheus diadema* Dana, variation in the dactyli of the third legs. *a*, Male, 19 mm. long, Kaneohe Bay, Hawaii; *b*, female, 24 mm. long, same locality; *c*, male, 15.5 mm. long, Tutuila, American Samoa; *d*, male, 18 mm. long, Midway Island; *e*, male, 17 mm. long, Tongatabu, Tonga. All drawn to the same scale.

stead, it should read: "Dactylus simple . . . as long as merus is broad."

Alpheus lanceloti Coutière
Fig. 8*a–k*

For synonymy, see Banner: 1958: 167.

LOCALITIES: 13 specimens, some ovigerous; Ahoolaka ("Sand Island") Kaneohe Bay, Oahu, Hawaii; collected from silty sand flats at tide level by A. H. Banner. Maximum length about 20 mm.

DISCUSSION: These specimens agree well with the original description by Coutière on the general configuration and most details; there are, however, some differences. The rostral front in general agrees with Coutière's description and figures (1905*a*: 900, pl. 63, fig. 39) but some variation occurs: the rostrum may be slightly longer, the rounded rostral ridge may not reach any further back than the middle of the orbital hoods, the frontal margin at either side of the rostrum may be definitely concave instead of almost straight, and finally the line or ridge at the inner margin of the orbital hoods is usually lacking. ("Le rostre est . . . séparé des voûtes orbitaires par un sillion. . . .") Slight and variable differences are similarly found in the proportions of the antennular peduncle and thoracic legs. In the large chela, as in the specimen already reported from Onotoa, the merus bears movable spines instead of teeth as shown by Coutière; moreover, the ischium of the same appendage bears three or four movable spines. The greatest difference is in the small chela of the male, which Coutière shows to be slender, with the fingers equalling the palm in length, while in these specimens the fingers are 1.2 times as long as the palm, slightly expanded in the middle, hooked on the end, and bear a fringe of setae, similar to a "balaeniceps-form," except that it does not cross over the superior face of the chela. The small chela of the females and immature males is similar to that drawn by Coutière. Coutière may have overlooked the sexual dimorphism. The small chela of the male from Onotoa was similar to the form described by Coutière. It should be noted that the large chela is laterally compressed, approaching the condition found in the Rapax group, but twisted, so that in these figures, and presumably those of Coutière, the compression is not shown.

In life the specimens had a basic light "sandy color," similar in hue to their environment; the chromatophores on their abdomens were in irregular and imperfectly defined bands. Their eggs were bright green.

These specimens were found burrowing into the coherent fine sand of a broad sand flat. While their burrows were not traced, from the depths of the excavations necessary to capture the shrimp it is estimated that they penetrate into the sand about 12–15 inches. In the same environment, but burrowing more deeply, are found *A. rapax* (Fabricius) and a callianassid shrimp.

The figures are included to complete the series of figures of Hawaiian species.

Brevirostris Group

Alpheus rapax Fabricius
Figs. 9*a–d*, 10*b*

For synonymy, see Banner, Pacific Sci. 10(3): 358, 1956.

LOCALITIES: About 40 specimens, Kaneohe Bay, Oahu, in shallow burrows on the inshore mud flats, intertidal zone; two specimens from deep sand burrows on Ahoolaka ("Sand Island") low in the intertidal zone, Kaneohe Bay, Oahu, Hawaii; collected by A. H. Banner, 1955, 1956.

DISCUSSION: These specimens seem to be of two different size ranges according to their habitats; those from the shallow burrows (possibly up to 6 inches deep in the mud flats, with *A. platyunguiculatus* (Banner) occupying deeper burrows reaching into buried coral heads) were mature individuals with the carapace lengths up to 7.6 mm., while the two from the deep burrows in the fine sand of Ahoolaka were found from 12 to 18 inches down (with *A. lanceloti* Coutière in shallow

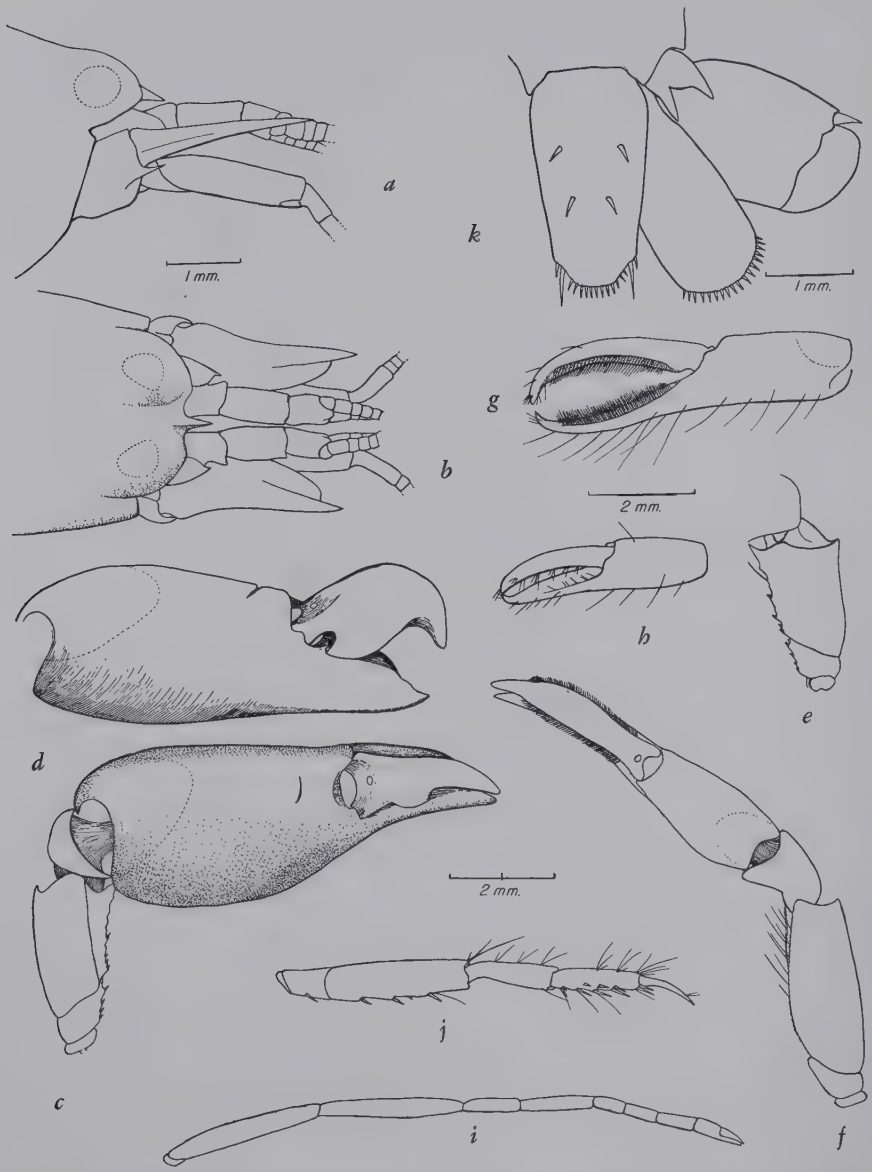

FIG. 8. *Alpheus lanceloti* Coutière. *a*, *b*, Anterior regions, dorsal and lateral aspects; *c*, large cheliped; *d*, large chela, inferior aspect; *e*, large cheliped, merus, medial aspect; *f*, small cheliped, male; *g*, small chela, male, inferior aspect; *h*, small chela, female; *i*, second leg; *j*, third leg; *k*, telson and uropods.

burrows) and were almost twice that size (carapace length of 13.5 mm., total length to 32 mm.). Because of this difference in size and habitat the individuals were carefully studied to see if any specific differences occurred between them. The large specimens were found to fall well within the range of variation of the small specimens. The difference in size may be due to the difference in habitat. The difference in the depth of burrows may be due to the underlying substrate of coral in the mud flats which prevents them from excavating their burrows as deeply as they can in the pure sand of the bar.

The variation in a group of 30 specimens, including the 2 large specimens, was tabulated with the following results.

Antennular peduncle: Second article from 1.4 to 2.5 times the length of the first. Third article from 0.6 to 1.1 times the length of the first.

Scaphocerite: Usually slightly to definitely longer than both carpocerite and antennular peduncle.

Carpocerite: Usually equal or subequal in length to the antennular peduncle; in two specimens, otherwise normal, equal in length to the scaphocerite, definitely longer than antennular peduncle.

Large chela: Total length usually 1.5 to 1.8 times breadth. Fingers usually 0.4 to 0.7 length of palm.

Small chela: Palm 1.2 to 1.5 usually 1.4, times as long as broad in males, 1.1 to 1.8, usually 1.3, times as long as broad in females.[3] Fingers 1.5 to 1.8, usually 1.7–1.8, times the length of palm in males, 1.4 to 1.8, usually 1.4–1.6, times length of palm in females.

Carpus, second legs: Second article 0.7 to 1.0 times length of first article, with most 0.8 times.

In one specimen a very peculiar large and small chela was noted. In this specimen the fingers of the large chela were 1.1 times the length of the palm, and the small chela was much thinner than usual, and not *balaeniceps*-shaped as would be expected for a male. (Fig. 9*c–d* contrasts these chelae with normal male chelae of approximately the same size.) All other characteristics are like those of the typical *A. rapax*. A similar condition has been previously reported. De Haan (1850: 178, pl. 45, fig. 4) described a new species, *A. digitalis*, separated from *A. rapax* only by the great elongation of the dactylus of the large chela. Coutière (1898*b*:248) examined the type of this species and two other species of the genus described on the basis of similar characteristics, and came to the conclusion that these were examples of regeneration where the development was arrested "à un stade

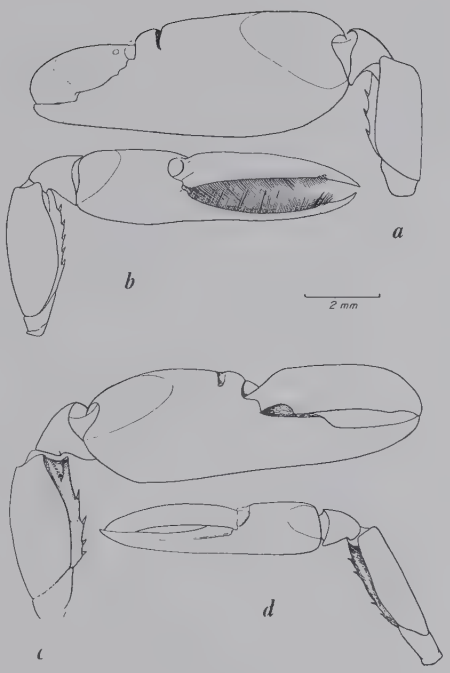

FIG. 9. *Alpheus rapax* Fabricius. Aberrant large and small chelae. *a*, *b*, Normal large and small chelae of male; *c*, *d*, aberrant large and small chelae, male. All drawn to same scale.

[3] In my original description of the Hawaiian specimens (1953: 128, top line, left column) there is an error for the palm was 1.5, not 2.5, times as long as broad.

moins profondément 'évolué' que sa forme habituelle," and that *A. digitalis* was a synonym of *A. rapax*. I believe a more logical explanation of this condition may be found in the process of either the normal replacement of a lost large chela, or the rather unusual replacement of both chelae. In the normal replacement of the large chela during successive molts, the small chela grows larger and takes on the appearance of the small chela; the condition drawn may be an intermediate stage where the small chela is regenerated, and the growing large chela has its size but not its final characteristics. In the replacement of both chelae, Darby (1934: 349, *et seq.*) reported that if the timing of loss of the individual appendages was controlled, they were replaced not by normal large and small chelae but by chelae of "intermediate" development.

Finally, many, but not all, of these specimens have the inferior external margin of the merus of the small cheliped bearing extremely fine and irregular movable spines or serrations; under ordinary magnification these are not noticeable, and even under 100 diameters of magnification it could not be discerned whether these projections were articulated. This, too, was not found in the regenerating chela mentioned above.

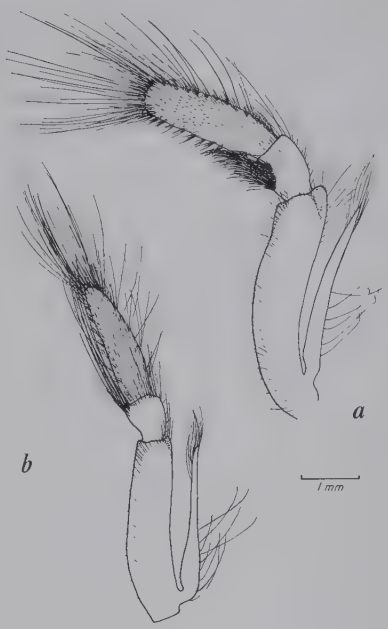

FIG. 10. *Alpheus platyunguiculatus* (Banner) and *Alpheus rapax* Fabricius, third maxillipeds, medial aspects. *a*, *A. platyunguiculatus; b*, *A. rapax*. Drawn to to the same scale.

Alpheus platyunguiculatus (Banner)
Fig. 10*a*

Crangon platyunguiculata Banner, Pacific Sci. 7(1): 130, fig. 47, 1953.

LOCALITIES: 8 specimens, the largest a 34 mm. ovigerous female, all collected from silt-buried coral heads in the intertidal mud flats behind the shoreward reefs of Kaneohe Bay, Oahu, Hawaii. Collected by A. H. Banner.

DISCUSSION: Since the collection of the five specimens upon which the original description was based, continuing search has been made for more specimens of this species. As explained in the original description, these shrimp appear to be confined to burrows in the muddy to sandy areas where the burrows can reach down through the loose substrate into buried coral heads. A section of inshore reef was found where the buried coral was loose and breakable; in this area these specimens were found, together with *A. rapax* (Fabricius). When only shallow holes were dug, several inches deep to the top of the imbedded coral, only *A. rapax* was found; when the imbedded coral itself was broken up from a depth of 8 inches or a foot, both *A. platyunguiculatus* and *A. rapax* were found. It appeared that the *A. rapax* was probably carried down from the sides of the excavation.

In the examination of these specimens an excellent specific characteristic was found to separate this species from *A. rapax*. In *A. platyunguiculatus* the middle article of the 3rd maxilliped bears a dense tuft of hairs, the longest reaching about one-third the length

of the ultimate article (Fig. 10*a*); in *A. rapax* this article bears a smaller group, not a tuft, of hairs, the longest of which reaches to the end of the ultimate article. In a few specimens of *A. platyunguiculatus* the tuft is not fully developed, but all lack the long setae of *A. rapax*.

Alpheus platyunguiculatus was separated from related species, especially from *A. sauvensis* de Man, on the basis of a series of minor differences in the proportions of the appendages.[4] This series of specimens was closely examined in those points of distinction, the results of which are given below:

	TYPE SPECIMEN	RANGE OF THIS SERIES
Ratio of lengths of first two antennular articles	1:1.3	1:1.4–1:2.0
Large cheliped		
Merus, length ÷ breadth	2.5	2.2–2.8
Number of meral spines	2	2–5
Chela, length ÷ breadth	2.3	2.1–2.6
Chela, finger length ÷ palmar length	0.5	0.4–0.7
Small Cheliped		
Merus, length ÷ breadth	2.6	2.0–2.8
Spines	4	2–5
Chela		
Palm, length ÷ breadth	1.5 female 1.6 female	1.5 sole male 1.3–1.6 females
Finger length ÷ palmar length	1.2 male 1.2 female	1.25 male 1.25–1.50 females
Second legs, ratio of first two carpal articles	1:2.3	1:1.85–2.3
Third legs		
Merus, length ÷ breadth	4.0	4.3–5.0

This range of variation destroys the value of most of the criteria set forth for the separation of *A. sauvensis* and *A. platyunguiculatus;* it also casts some doubts on the value of couplets used in de Man's key to this group. However, de Man (1908:110) specified that the dactyls of the third to fifth legs in his species were simple and rounded, and in all these specimens they are definitely flattened. Moreover, de Man did not describe the tuft of dense hairs on the penultimate joint of the third maxillipeds, and he did describe the terminal setae of the last article of this appendage as being over twice as long as the article, while in this species they are not even as long as the article. I believe, therefore, that this species is valid.

[4] In the tabulation on p. 132 of the original description the reference to the stylocerite should be to the scaphocerite, and in the comparison to *A. djeddensis* in the paragraph preceding the tabulation the text should read "small chela" instead of "third chela."

Edwardsii Group

Alpheus bastardi Coutière

Alpheus bouvieri var. *bastardi* Coutière, Soc. Ent. de France, Bul., 1898(5): 133, fig. 1a, 1898.

Alpheus bastardi Coutière, Fauna and Geog., Maldive and Laccadive Archipelagoes 2(4): 907, pl. 85, fig. 45, 1905.

LOCALITIES: 1 specimen, Station Y-111, Tomil Harbor, Yap Island, Caroline Archipelago, from holes in intertidal zone, rocky beach; collected by R. W. Hiatt, 1946.

DISCUSSION: This single specimen, a female, agrees perfectly with the short description and figures of Courtière. Unfortunately there is no male with which to confirm the identification.

Alpheus crassimanus Heller

Fig. 11*a–e*

For synonymy, see Banner, Pacific Sci. 11(2): 204, 1957.

LOCALITIES: 3 specimens from Station Y-111, collection data as above. One specimen, Station 2015, Otikaheru Island, Tuamotu Archipelago, on coral stones, under surface of muddy sand, near shore of brakish enclosed lagoon; collected by J. E. P. Morrison, July 29, 1952.

DISCUSSION: Most of the previous studies on this species have indicated that the small chela of the male not only has the dactylus subspatulate and fringed with long setae, but also that the palm bears sculpturing (see de Man, 1911, p. 417; Bate, 1888: pl. 99, fig. 2;

Coutière 1899: fig. 293). Yet the illustrations showed slight differences in the sculpturing (contrast Bate, fig. 2k to Coutière, *loc. cit.*). In contrast, the specimens reported from Hawaii (Banner, 1953: 134) did not show the sculpturing, nor did those reported from Arno and Onotoa (Banner, 1957: 204; 1958: 168).

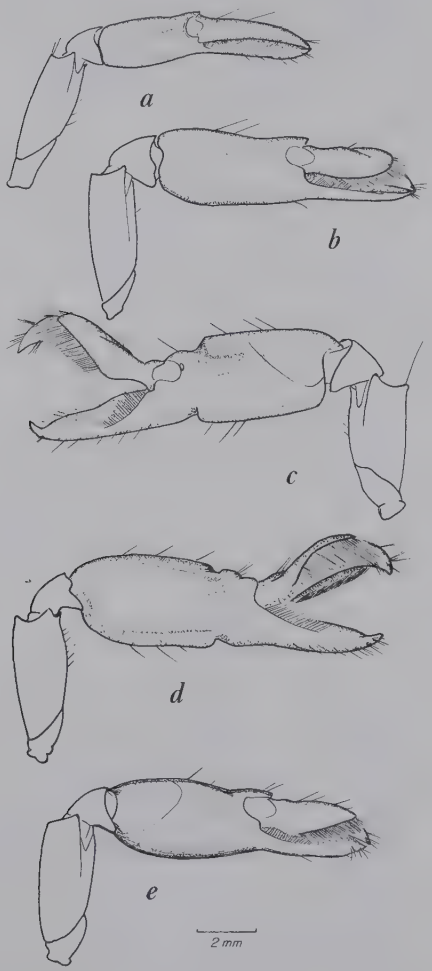

FIG. 11. *Alpheus crassimanus* Heller. Variation in form of small chelae. *a*, 22 mm. ovigerous female; *b*, 22 mm. male; *c*, 27 mm. male, lateral aspect; *d*, same, medial aspect; *e*, 24.6 mm. male. Specimens shown in *a–d* from Yap, *e*, from Hawaii; all drawn to same scale.

The three specimens from Yap indicate a possible reason for this difference. One of the specimens is an ovigerous 22 mm. female, which shows a slight trace of sculpturing in a shallow, ill-defined depression located longitudinally on the upper surface of the palm. The male of the same size has the characteristic dactylus of the adult male, yet the palm, like that of the female, bears only a slight longitudinal depression. However, in the 27 mm. male the palm is strongly sculptured. It is very roughly triangular in cross section, with the upper medial and lateral faces bearing extensive depressions that are quite well deliminated (although not as definite as the corresponding depressions on the large chela); these are connected across the superior margin by a rounded, saddlelike transverse groove. On the inferolateral margin there is a strong shoulder; the inferior surface of the chela is flattened and demarked by abrupt but rounded margins; the inferolateral shoulder does not continue on the inner face.

Specimens from Hawaii were re-examined, and while the smaller males show almost no trace of the sculpturing, the largest male available (24.6 mm. long, collected in the mud flats at Heeia, Kaneohe Bay, Oahu in about plus 1 to 2 ft. tide zone) shows sculpturing similar to that of the 22 mm. Yap specimen.

Inasmuch as specimens less than 20 mm. long are often ovigerous, and inasmuch as specimens up to 44 mm. long have been reported (de Man, 1902: 880), it appears that the younger, but mature, males bear the subspatulate dactylus but may be entirely lacking in the sculpturing of the palm, while larger males develop the sculpturing. It is likely that the point of transition between the two forms may be around the body length of 25 mm., although this size may vary in different geographic areas. For example, none from Hawaii appear to reach the necessary size, while the specimen reported by de Man from Makassar (*loc. cit.*) evidently had the sculpturing at a body length of 25 mm.

It may be that this is the wrong conclusion to draw from these specimens. Certainly two male specimens are not enough to prove or disprove the relationship. Only when a series of specimens of different body lengths are available can it be safely said that this is or is not a growth difference.

It should also be noted that the merus of the larger chelipeds of the 22 mm. female and the 27 mm. male bear a small acute tooth at the termination of the inferior internal margin, while the 22 mm. male, like those from Hawaii, lack this tooth.

The one specimen from the Tuamotus is a smaller male and similar in the form of the small chela to those from Hawaii.

Alpheus strenuus Dana

For synonymy, see Banner, Pacific Sci. 11(2): 204, 1957.

LOCALITY: 1 specimen, Station Y-122 from Tomil Harbor, Yap Island, Caroline Archipelago, in shallow burrows, intertidal zone; collected by R. W. Hiatt, 1946.

Alpheus pacificus Dana

For synonymy, see Banner, Pacific Sci. 10(3): 362, 1956.

LOCALITY: 2 specimens from Midway Island, Hawaiian Archipelago; collected by Y. D. P. Speicer, 1941.

Alpheus malabaricus (Fabricius) *mackayi* subsp. nov.

Fig. 12*a–n*

Astacus malabaricus Fabricius, System. Ent. p. 415, 1775.

Alpheus malabaricus Fabricius, Sup. Ent. System., p. 405, 1798.

Alpheus malabaricus Henderson, Zool. Soc. London, Trans., II, 5: 434, pl. 40, figs. 1–3, 1893. [Species reestablished and redescribed.]

Alpheus malabaricus de Man, Siboga Exped. 39a[1] (2): 429, 1911. [New subspecies with separate synonymy.]

Alpheus malabaricus Barnard, South African Mus., Ann., fig. 142 l-n, 1950.

Crangon species, McKay, Canad. Field-Nat. 61(4): 135, pl. 1, 1947.

TYPES: Holotype, an ovigerous female 37.8 mm. long; allotype, a male 27.7 mm. long; both collected by Donald C. G. MacKay in Wailupe fish pond, Oahu, Hawaii.

DESCRIPTION: Orbital hoods and rostrum protruding far beyond anterolateral margins of carapace. Orbital hoods inflated, high, rounded; rostrum short, not reaching beyond anterior margin of orbital hoods, carina short, rounded, not reaching to middle of orbital hoods; interorbital area behind termination of carina flat, anteriorly abruptly demarked from convexity of orbital hoods.

Antennular peduncle with second article about 2.4 times as long as broad, about twice length of visible portion of first article and not quite 3 times length of third article. First article terminating in high setose crest on superior margin; basicerite broad, flat, with small anterior tooth not reaching to end of first article. Basicerite with acute lateral tooth. Scaphocerite reaching to beyond end of antennular peduncle, squamous portion broad, slightly narrowing distally, and exceeded by the lateral spine; lateral spine curved inward at tip. Carpocerite reaching to end of lateral spine of scaphocerite.

Large chela of male and female of similar proportions, and almost identical size in spite of difference in body lengths. Merus with outer face 1.7 times as long as broad; superior margin ending distally in slight projection; inferior internal margin terminating in strong acute tooth, otherwise unarmed. Carpus of usual form. Large chela 2.4 times as long as maximum width, tapering towards fingers, with maximum width of fingers 0.66 as wide as palm; fingers strong, occupying the distal 0.3 of chela (about half as long as palm). Palm with rounded depressed areas on either face, both roughly triangular; superior margin of palm ending in shoulder overhanging shallow, rounded groove that connects de-

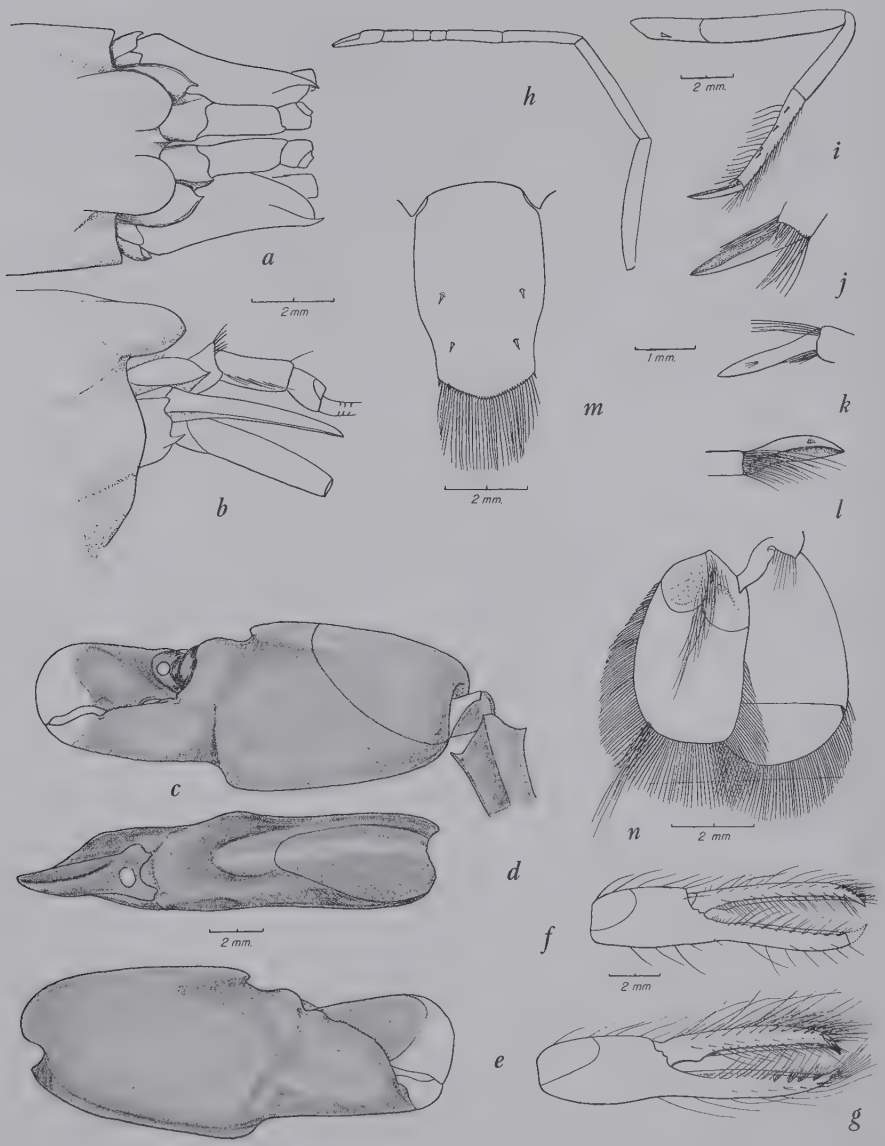

FIG. 12. *Alpheus malabaricus* (Fabricius) *mackayi* subsp. nov. *a*, *b*, Anterior regions, superior and lateral aspects, setae not shown; *c*, *d*, *e*, large chela, lateral, superior and medial aspects; *f*, small chela, male; *g*, small chela, female; *h*, second leg; *i*, third leg; *j*, *k*, *l*, dactylus, third leg, anterior, superior and posterior aspects; *m*, telson; *n*, uropod, showing proximal concavities.

pressed areas on either face; inferior margin terminating, almost right angled, in strong shoulder on outer face.

Small chelae also similar in both sexes. Merus unarmed on inferior internal margin. Palm slender, rounded, without sculpturing. Fingers 1.4 times length of palm in female, 1.7 times length of palm in male, straight except for slightly hooked tips, both movable and fixed fingers rounded on outer portion of opposing faces, bearing a sharp cutting edge on inner margin; dactylus bearing a low rounded tooth proximal to cutting edge.

Carpal articles of second legs with the ratio: 10:7.6:2.0:2.3:4.3; chela, in same ratio, 1.7.

Third and fourth legs with ischium bearing weak spine; merus 6 times as long as broad, unarmed; carpus 0.6 as long as merus, without distal teeth or projections; propodus 0.75 as long as merus, bearing 6 feeble spines and numerous long setae; dactylus 0.3 as long as merus, strongly curved in superior view, roughly triangular in cross section, with both superior faces somewhat convex, inferior face broad and flattened. Fifth leg with brush on propodus strongly developed.

Telson 2.4 times as long as posterior margin is broad, 1.3 times as broad anteriorly as posteriorly; in dorsal view, anterior 0.6 with slightly convex margins, without taper, then tapering abruptly to posterior portion with parallel margins; in lateral view, middle of lateral margin strongly depressed; tip strongly arcuate. Dorsal spinules feeble; inner pair of posterolateral spinules so slender that they can be confused with terminal setae; terminal setae numerous and heavy; posterior margin also armed with series of minute spinules. Outer uropod with spine on shoulder slight. Inner uropod with a shallow but well-demarked basin to accommodate depressed lateral margin of telson.

DISCUSSION: These specimens agree very well with the species *A. malabaricus* as redescribed by Henderson, and with the subspecies described by de Man (*loc. cit.*), except in the length of the rostrum and the relative proportions of the small chela; apparently all are similar in form of the dactylus of the third legs, in the general shape of the large chela, etc. However, all specimens of *A. malabaricus* except that described and figured by Barnard from South Africa (*loc. cit.*), have longer rostrums, and in none are the fingers as short when compared to the palm. Both reported subspecies have fingers on the small chela that are gaping instead of straight. The habitat of these specimens—the thick soft mud of a fish pond—and those reported by Henderson from India are also similar.

Because of their great similarities it is not logical to consider these specimens as other than a geographically isolated subspecies; it may be that when other specimens are found between Hawaii and India intergrading specimens will be found.

The type locality, Wailupe fish pond, no longer exists. It was filled in and is now used for homesites, the area being called Wailupe Peninsula. Presumably the subspecies exists elsewhere in the Hawaiian Islands, but it has not yet been found in other areas.

THUNOR Armstrong

Thunor microscaphis sp. nov.
Fig. 13*a–i*

Thunor sp. Banner, Pacific Sci. 10(3): 367, fig. 23a–e, 1956.

TYPE SPECIMEN: A 9.5 mm. male from Station 827, Likiep Atoll, Marshall Islands, USNM 194726; collected by S. V. MacNeil.

DESCRIPTION: Specimen with cephalothorax preponderant, abdomen reduced, only slightly more than equal in length to carapace.

Anterior carapace distorted in specimen with folds and wrinkles permitting the eyes to be partially exposed. Rostrum obtuse, short, not reaching beyond anterior margin of orbital hoods, and bearing low, rounded carina reaching to slightly past middle of orbital hoods. Orbital hoods large, inflated, evenly rounded anteriorly.

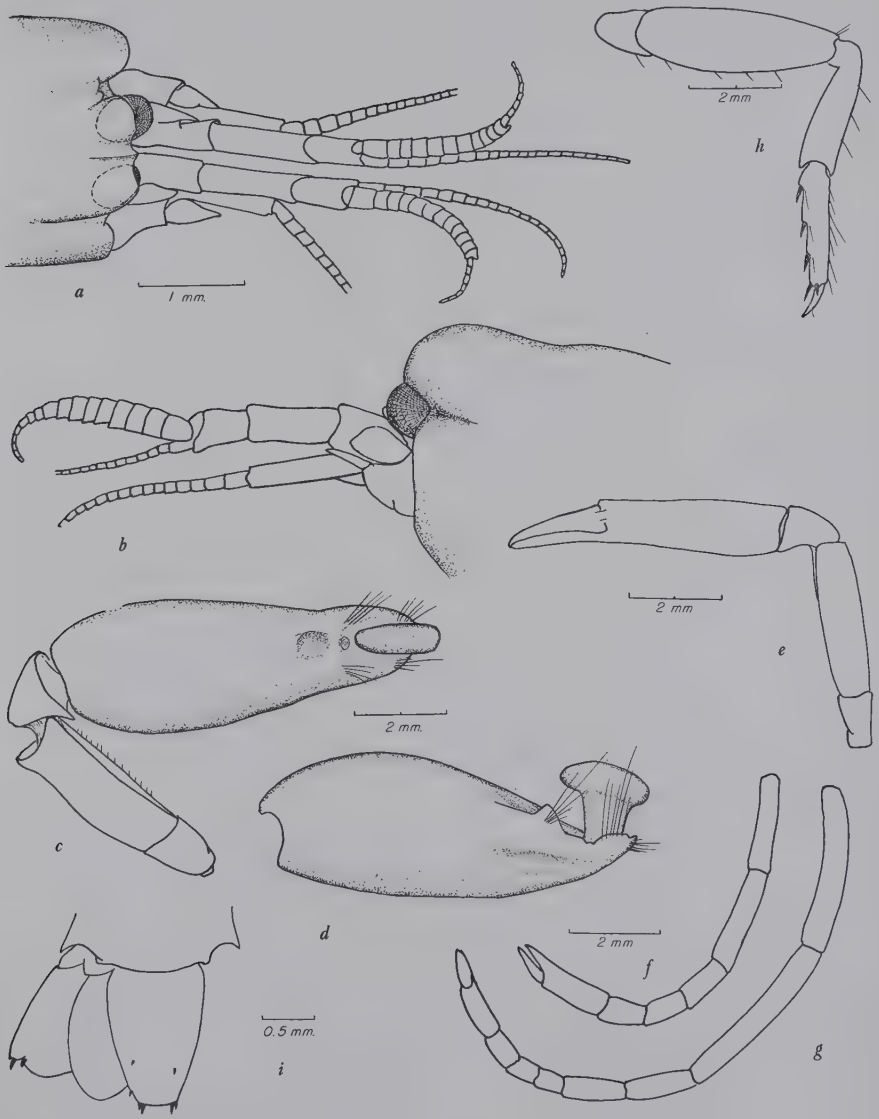

FIG. 13. *Thunor microscaphis* sp. nov. *a*, *b*, Anterior regions, superior and lateral aspects; *c*, *d*, large cheliped; *e*, small cheliped; *f*, second leg, left, carpus to dactylus; *g*, second leg, right, ischium to dactylus; *h*, third leg; *i*, telson and uropods.

Antennular peduncle with second article 1.7 times length of first article; third article subequal to first; second article 3.5 times as long as broad. Stylocerite assymetrically developed, with that on left almost rounded anteriorly and reaching about 0.7 the length of first article; that on right anterior irregular (but rounded) reaching only a little more than 0.5 length of first article.

Scaphocerite reduced to bract which reaches on left to end, on right to slightly beyond end of first antennular article. Basicerite unarmed. Carpocerite reaching 0.6 length of second antennular article. Antennal flagellum elongate.

Large chela 2.7 times as long as broad, with fingers occupying the distal 0.2; margins mostly regular and strongly tapering. Distally chela with a deep pit proximal to articulation of dactylus to accommodate protruding margin of dactylus; lateral and proximal to articulation of dactylus is located a shallow depression with poorly defined margins. Fixed finger very short. Dactylus hammer-shaped, with distal margin swollen and rounded, proximal portion broad and thin. Carpus of usual form. Merus about 0.4 length of chela, with outer face 3.5 times as long as broad; distally unarmed; inferior internal and external margins sharp; inferior internal margin bearing 13 slight and feeble spines.

Small chela 5 times as long as broad, with the simple fingers occupying the distal 0.35. Merus 0.55 length of chela, 0.25 as long as broad, unarmed.

Second legs assymetrical, with left as long as body, and right a little over half as long. Carpal articles of right legs with ratio: 10:9:4:5:6; left leg with first article slightly shorter, relatively.

Third leg with ischium unarmed; merus unarmed, 3.2 times as long as broad; carpus with distal angles rounded; propodus bearing 3 single inferior spines and paired spines distally; dactylus simple and curved.

Outer uropod bearing a single lateral spine without articulation, inner unarmed. Telson 3.5 times as long as tip is broad, 1.8 times as broad anteriorly as posteriorly; sides slightly curved. Dorsal spines abnormal, with anterior left about 0.7 length posterior from articulation, posterior left located on margin; anterior right posterior to corresponding left, posterior right missing.

DISCUSSION: This single specimen appears to be of the same species as the two fragmentary specimens previously described but not named from Saipan (Banner, *loc. cit.*). A number of slight differences are found between the two forms: the length of the interorbital carina, the proportion of the articles of the antennular peduncle, the ratio of the carpal articles of the second leg (only one second leg remained on the two Saipan specimens), the armature of the propodus of the third legs, and the proportions and armature of the telson. These differences, most of them in parts that have been found to be variable in *T. idiocheles* (Courtière) and *T. rathbunae* (Schmitt), as well as in related species of the Obesomanus group of *Alpheus*, are probably without significance. Another difference between the two lies in the development of the antennal peduncle: in the male specimen from Saipan the scaphocerite reaches to the middle of the second article of the antennular peduncle, and the carpocerite reaches to the end of the same article, while in the female from Saipan the developement of these is shorter and more degenerate than that found in the male. As this male is similar to the Saipan female, the difference is obviously not sexual dimorphism, but may show the variability of the development of this appendage; however, the two Saipan specimens may be of different species. A final difference is found in the merus of the large chela, which in this specimen bears 13 feeble spines, and in the Saipan specimen bears a few bristles in corresponding locations. Opposed to these slight and seemingly insignificant differences are many and great similarities, as can best be seen by comparing the figures of the two forms.

This species plainly belongs to *Thunor* if

that genus is to be accepted, for it lacks the anal tubercles and the articulation of the outer uropod; in addition the specimens lack the ocular beak and in two of the three specimens the cardiac notch is lacking.

Within the genus, *T. microscaphis* is best distinguished from *T. idiocheles* by the form of the large chela, for in this species the dactylus is formed like a two-headed hammer, and the superior surface of the chela bears a marked depression to accommodate the superior projection of the dactylus when that article is flexed. In *T. idiocheles*, the dactylus of the large chela lacks this superior projection and there is no corresponding depression of the palm. From *T. rathbunae* this species is distinguished by the presence of a small rostrum as well as by the form of the large chela and the relatively greater length of the small chela.

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Four New Species, a New Genus, and a New Suborder of Hawaiian Fishes[1]

WILLIAM A. GOSLINE[2]

THE DESCRIPTION of new taxa in a "Handbook of Hawaiian Fishes" recently submitted for publication was considered inadvisable. Certain of these are grouped together here, i. e., three new species of Gobiidae (*Quisquilius aureoviridis*, *Q. limbatosquamis*, and *Hazeus unisquamis*), a new genus and species of Callionymidae (*Pogonymus pogognathus*), and a new suborder of Perciformes (Schindlerioidei) erected for the fishes of the genus *Schindleria*.

Family GOBIIDAE, Genus QUISQUILIUS

The two new species of *Quisquilius* described below can be assigned to that genus with considerable assurance, as the type species, *Q. eugenius*, is another Hawaiian form of which numerous specimens are available. The characteristics listed in the following paragraph are held in common by the two new species and *Q. eugenius*.

No hairlike or flaplike appendages on the head or shoulder girdle. No serrations or spines on the preopercle. Maxillary not prolonged posteriorly. No V-shaped notch in the tip of the lower jaw. No teeth on the vomer. Teeth in both jaws in several rows, those of the outer and inner rows enlarged and spaced at intervals. One or two fanglike teeth in the outer row at each anterolateral angle of the lower jaw. Tongue usually with a slight to broad notch in the tip. Cleft of the mouth more or less oblique. Both nostrils in tubes, the anterior at least twice as far from the posterior as from the groove behind the upper lip. No pores on the head. The rows of papillae (not shown in Fig. 2) are in very uniform alignment. There is one pair on the posterior portion of the interorbital and two rows of about 5 papillae each on the flesh covering the premaxillary pedicels. A series of about 5 large, widely spaced papillae borders the orbit below. A row or pair of rows runs backward from the eye just above the upper border of the opercle. Two horizontal rows on cheek, the upper sometimes extending all the way across but the lower ending on middle of cheek. A verticle row down front of operculum with two branches running back or down and back from it. One or two rows along the lower border of the preopercle. One row of papillae above and two below enclose the corner of the mouth. Two rows on the gular membrane, one on each side. Gill openings extending down to below the preopercular border, the distance between their lower ends equal to or less than an eye diameter. Ten or more developed gill rakers on the lower limb of the outer arch. Scales ctenoid, those on the body not especially enlarged posteriorly. Scales on top of head extending forward nearly to eyes, but no enlarged scales just behind eyes. First dorsal fin with 6 spines. First spine in both dorsal fins with a flexible tip. Caudal rounded, not longer than the head length. Pectoral without silky rays above. The united pelvics without a basal frenum, the membranes uniting the inner rays easily torn (as it apparently was in the holotype of *Q. eugenius*).

Examination of numerous specimens of *Q. eugenius*, 15 to 45 mm. in standard length, indicates no great sexual dimorphism. Over the available size range there is also no great differentiation in sensory papilla pattern. However, the cheek squamation does not appear until well after all of the other scales have formed.

[1] Contribution No. 112 of the Hawaii Marine Laboratory in cooperation with the University of Hawaii, Department of Zoology and Entomology. Manuscript received December 18, 1957.

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Among Hawaiian gobies *Zonogobius* (as represented by *Z. farcimen*) seems to be the closest relative. These two genera are set off from other Hawaiian gobies by the following features: no pelvic frenum; two longitudinal series of papillae on the flesh covering the premaxillary pedicels; and 10 or more developed gill rakers.

Of the three Hawaiian species of *Quisquilius*, *Q. eugenius* is an abundant shallow-water fish inhabiting areas of dead coral. It seems to be restricted to depths of less than 15 feet. The other two species are in general deeper-water forms, though the type of *Q. aureoviridis* was collected in a tide pool with a maximum depth of 7 feet.

Quisquilius aureoviridis sp. nov.
Fig. 1, Table 1

HOLOTYPE: USNM 175013, 37.1 mm. in standard length taken in a rotenone station at Pupukea, Oahu, Territory of Hawaii by Gosline, *et al.*, Dec. 23, 1949.

PARATYPES: USNM 175014, 1 specimen. 36.2 mm., about 1 mi. north of Kailua, Hawaii, T. H., Gosline, *et al.*, June 19, 1953; University of Hawaii No. 1703, 8 specimens, 21.0–27.2 mm., off Waikiki reef, Oahu, T. H., Gosline, *et al.*, Dec. 31, 1952.

Depth of body contained about 4 times in the standard length.

Head somewhat wider than deep, its greatest depth contained about 1.5 times in the head length. Mouth oblique, the lower jaw protruding. Front of mouth about on a level with the middle of pupil; rear of jaw about reaching to below front border of pupil. Eye bordered by a shallow groove posterodorsally, its diameter contained about 4 times in head in a 2-inch specimen. Least distance between eye and groove behind upper lip contained a little over 2 times in the eye diameter. Anterior nostril placed just above the groove behind upper lip, the posterior above the level of the top of pupil. Interorbital gently concave, not in a deep trench between the eyeballs, its width contained about 4 times in the eye diameter. Thirteen moderate, pectinate gill rakers on the lower limb of the outer arch in one specimen. Tongue rounded but usually with a central notch at tip.

Body completely scaled, those scales above the pectoral base rather irregularly placed. A few scattered rows of papillae crossing certain of the body scales. Head scaled forward to the groove behind each eye. No scales on cheek or operculum. Thirty to 33 scales in a longitudinal series, 9 or 10 in a transverse series; about 13 predorsal scales.

Some of the spines in the first dorsal filamentous. Second dorsal with a spine and 10 or 11 soft rays. Anal with a spine and 8 or 9 soft rays. Pectoral with about 19 rays.

TABLE 1
CERTAIN COUNTS IN THREE HAWAIIAN SPECIES OF *Quisquilius*

SPECIES	LATERAL LINE SCALES*								TRANSVERSE SCALE ROWS†					TOTAL 2ND DORSAL RAYS				TOTAL ANAL RAYS		
	26	27	28	29	30	31	32	33	7	8	9	10	11	10	11	12	13	9	10	11
Q. eugenius		1	1	3							2	2	1			4	1	1	3	1
Q. aureoviridis																				
Holotype								1				1				1			1	
Paratypes				1	1	1		1			3	2			2	3		3	2	
Q. limbatosquamis																				
Holotype		1							1						1			1		
Paratypes	2	4							3	3				6				5	1	

* Counted from the upper angle of the gill opening to the crease at the end of the hypural fan.
† Counted from the beginning of the anal upward and forward to the dorsal base.

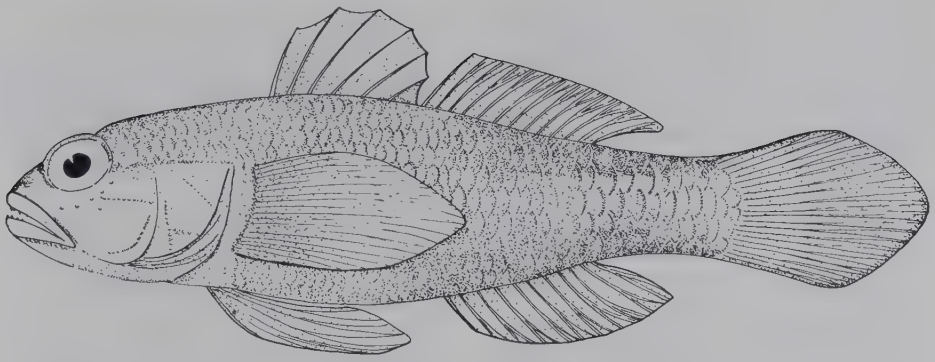

FIG. 1. *Quisquilius aureoviridis*, holotype.

Color in life yellowish green to yellowish brown with faint slightly darker vertical bars. In alcohol a broad, lighter longitudinal bar becomes apparent along the middle of the body posteriorly. Fins light or dusky. Small specimens show traces of dark vertical bars on the head.

Quisquilius aureoviridis differs from *Q. eugenius* most notably in interorbital structure. In the latter species the eyes are raised, leaving a deep, narrow trench between them, the bottom of which is hardly visible; in *Q. aureoviridis* the eyes are little raised above the level of the relatively broad interorbital. In *Q. eugenius* the scales on the cheek and opercle are prominent in adults; in *Q. aureoviridis* they are absent. Finally, the two species may at once be separated in life by coloration, for *Q. eugenius* is a brownish black with vertical stripes.

Koumans (1953: 131) has synonymized four other species with *Q. eugenius*. Of these, three at least—*Q. cinctus*, *Q. naraharae*, and *Q. profundus*—do not seem to belong there. They appear, on the contrary, to be somewhat nearer *Q. aureoviridis* at least in the lack of squamation on the cheek and (usually) on the operculum. All of them differ from *Q. aureoviridis*, however, in having the body dark with light bands and in the punctate soft dorsal and anal fins.

Quisquilius malayanus and *Q. macrophthalmus* appear to be relatively large scaled forms, as is the species described below.

Aureoviridis = (L.) yellow green.

Quisquilius limbatosquamis sp. nov.
Fig. 2, Table 1

HOLOTYPE: USNM 175012, 20.0 mm. in standard length, taken in a rotenone station about 2 mi. west of Haleiwa, Oahu, Territory of Hawaii by Gosline, *et al.*, July 23, 1955.

PARATYPES: University of Hawaii No. 1704, 8 specimens, 15.6–18.5 mm., off Waikiki reef, Oahu, T. H., Gosline, *et al.*, Dec. 31, 1952.

Depth of body contained 4.5 times in the standard length.

Greatest width of head considerably greater than greatest depth of head, the latter contained about 1.9 times in the head length. Mouth oblique, the lower jaw protruding. Front of mouth about on level with center of pupil. Rear of jaw below front of pupil. Eye not surrounded by a recessed groove above or posteriorly, its diameter contained about 3.7 times in the head length. Smallest distance between eye and groove behind upper lip contained about 2.5 times in the eye diameter. Anterior nostril about ⅓ as far from the groove behind upper lip as from the posterior nostril. Posterior nostril slightly above top of pupil. Interorbital narrow, not in a deep recess, its width contained perhaps 5 times in

the eye diameter. No pores on head. Rows of papillae on head less markedly developed than in *Q. aureoviridis*. Ten gill rakers on the outside row of the lower limb of the first arch. Pseudobranch composed of 4 lobes. Tongue as seen from below rounded but with a slight indentation in middle.

Body completely scaled except apparently on the middorsal ridge that runs about one eye diameter forward from the first dorsal fin. Head scaled forward to an imaginary line drawn across between the rear of the orbits. Cheek and opercle scaleless. Twenty-six or 27 scales in a longitudinal series; 7 or 8 transverse rows; predorsal scale row incomplete. Scales ctenoid, except perhaps for those on breast.

None of the dorsal spines filamentous. Membrane between the two dorsals not quite connecting them. Second dorsal with a spine and 9 or 10 rays. Anal with a spine and 8 rays. Pectoral 19 or 20.

Color light with a light, dark-bordered vertical band crossing the nape and enclosing the pectoral base. Behind this are 6 vague dark vertical bands, one of these at caudal base, the others darkest on the middorsal and midventral lines. Each scale on the body completely and prominently outlined by a series of large melanophores. Dorsal fins, particularly the first, with dark smudges at the base of the rays. Soft dorsal rays speckled. Head with traces of 3 broad vertical bands running down cheek and operculum.

This species was taken along with *Quisquilius aureoviridis*. It resembles that species rather than *Q. eugenius* in that the orbits are not partially enclosed in a deep trench and in the absence of scales on the cheek and head. However, *Q. limbatosquamis* differs from both the other Hawaiian species of the genus in the somewhat flatter head, in having a triangular naked area on the top of the head between and behind the eyes, in having a naked ridge extending forward from the first dorsal, in the larger scales and fewer dorsal rays. In color *Q. limbatosquamis* differs from the other two in having each of the scales distinctly outlined by a series of melanophores.

Of other described species *Q. limbatosquamis* seems to differ from *Q. malayanus* in color and from *Q. macrophthalmus* in the far higher pectoral count.

Limbatosquamis = (L.) edged scale.

Family GOBIIDAE, Genus HAZEUS

The relationships of the fish described below are most obscure, at least to the present author. It has been placed in the genus *Hazeus* because nothing better could be found. As one source of confusion this author has never seen the type species of *Hazeus*, *H. otakii* Jordan and Snyder (1902: 51, fig. 3). As another, the genus has frequently been considered a synonym of *Gnatholepis*, e.g., by Jordan and Evermann (1905: 487) and by Koumans (1931: 86; 1953: 168), but until it can be determined what fish *G. anjerensis*, the type species of *Gnatholepis*, represents there can be no final decision on the matter.

Hazeus unisquamis sp. nov.
Fig. 3

HOLOTYPE: USNM 175009, 18.2 mm. in standard length, taken by means of rotenone in a cut in the reef about 200 yds. west of Diamond Head, Oahu, Territory of Hawaii, by Gosline and class, May 16, 1950.

Depth of body contained 4 times in the standard length. Depth of caudal peduncle contained about 2.5 times in its length.

Head considerably wider than deep, the greatest depth of head contained about 1.4 times in the head length. Cleft of mouth broad and very slightly oblique, the lower jaw somewhat projecting. Front of mouth about on a level with lower border of pupil; maxillary reaching to below middle of eye. Upper lip narrow, its greatest width somewhat less than that of lower lip. Eye directed superolaterally, its diameter contained about 2.2 times in the head length. Smallest distance between eye and groove behind upper lip contained about 4 times in the eye diameter. Both

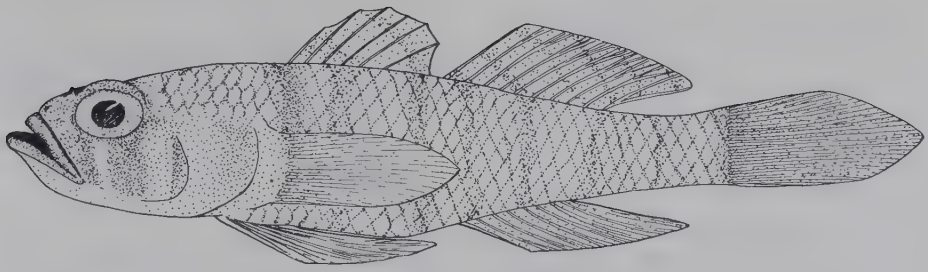

FIG. 2. *Quisquilius limbatosquamis*, holotype.

nostrils bordered by a low, raised collar, the anterior slightly nearer the posterior than the groove behind upper lip. Interorbital very narrow, hidden in a groove between the raised orbital borders. No pores on the head. Superior borders of orbit raised in a series of low flaps, these bordered behind by a groove; behind the interorbital region this groove is also bordered on the side away from the eye by a series of raised, scalelike flaps. No papillae on top of head, snout, or around eye, but two rows following the lower portion of the preopercular border and extending forward below the ramus of the lower jaw; another weakly developed vertical row on anterior portion of operculum. Gill cover free from the isthmus, the gill openings extending far forward about to below front of pupil. Ten widely spaced, pectinate gill rakers on the lower limb of the outer arch. Pseudobranch consisting of 5 lobes. Tongue with a broad, shallow median indentation as seen from below. Teeth in a narrow band in both jaws, some of the teeth on the inner border of the band somewhat enlarged; none of the outer teeth in either jaw especially enlarged.

Top of head scaled forward to the eye. Operculum almost completely covered by about 12 large, ctenoid scales. A single, large, embedded scale on the upper portion of each cheek. Twenty-six scales in a longitudinal series from above the upper end of the gill cover to the base of the caudal; 6 scales in a transverse series. Breast in front of pelvics without scales.

All of the fins with short, heavy rays maintained more or less erect. First spine in both dorsal fins more slender than the succeeding rays and with a soft tip. Dorsal VI-I,7. Anal I,7. Pectoral without silky rays above, with 18 rays in all; the upper 11 rays branched, the lower 7 simple, swollen and extending somewhat beyond the interradial membranes. Pelvics united, with a thin, smooth-edged frenum anteriorly.

In alcohol the only prominent marks are narrow black borders to the two dorsal fins and a blackish bar across the caudal peduncle just in front of the caudal base; chromatophores are scattered more or less evenly over the rest of the body and head, giving a plain gray ground color.

So far as I can see from the species descriptions available to me *Hazeus unisquamis* may be differentiated from related forms by having only a single scale on the cheek, dark borders to the two dorsal fins, and only 7 soft rays in the dorsal and anal.

Unisquamis = (L.) one scale, in reference to the single cheek scale.

Family CALLIONYMIDAE

POGONYMUS gen. nov.

TYPE SPECIES: *Pogonymus pogognathus* sp. nov.

Head and body depressed forward of the anal origin, compressed posteriorly. Head flat above, the eyes completely separated by a slightly concave interorbital area. No supraorbital tentacle. Preopercular process with an

upturned tip and with one additional dorsally directed spine ahead of tip; without an antrorse spine on its outer surface. Gill opening a small hole beneath the dorsal portion of the well-developed opercular flap. Lower jaw included, without a reverted lip but with a fringe of about 12 to 16 forwardly projecting papillae the tips of which extend beyond the upper jaw when the mouth is closed. Teeth elongate, in one or a few rows in both jaws, those above pointing backward, those below projecting up and back. A single lateral line running along sides, without notable side branches except for one at the rear, which forms a saddle across the caudal peduncle. Two dorsal fins, the first very low, of 2, 3, or 4 spines none of which reach the second dorsal origin when the first dorsal is depressed. Rays of second dorsal unbranched except for the last. All of the anal rays branched at tip, except for the last, which is divided to the base. Pelvic fins without separated rays and not attached to the middle of the pectoral fins by a membrane.

Judging from the keys to callionymid genera given by Schultz and Woods (1948: 419–420) and others, *Pogonymus* is most closely related to *Eleutherochir*. It differs from that genus and most other callionymids in the presence of a fringe of papillae on the lower jaw and in having the anal, but not the soft dorsal, rays divided at the tips.

Pogon = (Gr.) beard; onyma = (Gr.) name.

Pogonymus pogognathus sp. nov.
Fig. 4

HOLOTYPE: USNM 175010, a nearly ripe female 25 mm. in standard length, taken in 3 to 10 ft. of water in a small cove just west of Hanalei Bay, Kauai, Territory of Hawaii, by Gosline and Ohai, June 19, 1952.

PARATYPES: USNM 175011, 5 specimens, 15–21 mm.; University of Hawaii No. 1626, 34 specimens, 11–22 mm., all with the same data as the holotype.

Head broad and flat, its greatest depth contained about 1.6 times in its greatest width, which in turn is contained about 1.2 times in the head length to the end of the opercular flap. Eyes large, contained about 4 times in the head length, not projecting above the dorsal surface of the head, separated by a bony interorbital that is about equal to a pupil diameter in width and that contains two median pores. Snout broad and blunt, its length about ⅔ an eye diameter. Gape nearly twice as broad as deep, the maxillary reaching about to the anterior border of the eye when the mouth is closed. Gill covers attached to one another below by a free fold across the isthmus.

FIG. 3. *Hazeus unisquamis*, holotype.

Lateral line dropping down to the midsides about at the pectoral tip, giving rise to about 15 pores along its length, some of these slightly above the lateral line and others slightly below; terminating posteriorly about halfway out along the caudal rays.

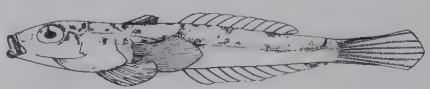

FIG. 4. *Pogonymus pogognathus*, paratype.

First dorsal originating about ⅓ of the way back along the standard length, its rays low and rather tightly bound to the midline of the back by the membrane behind the last ray. Longest dorsal spine considerably shorter than the distance between dorsal fins. Soft dorsal with 9 or 10 rays, lying somewhat ahead of anal, its last ray not nearly reaching caudal base when depressed. Anal with 9 or 10 rays, the tip of the last about reaching caudal base.

Caudal fin slightly shorter than the head length, with 6 principal rays, all of which are somewhat branched at tip, the outermost least so; 10 caudal rays in all, the outermost short, splintlike, and unsegmented. Pelvic fins with a spine and 5 branched rays, the fourth of which is the longest. Pectoral with about 19 rays, the longest of which reach about to above the anal origin.

A 15 mm. (standard length) specimen has black spots at the base of each soft dorsal and anal ray and another at the base of tail. Between 15 and 20 mm. these markings fade, so that the specimens are a plain yellowish brown except for some incipient markings on the back and on the first dorsal. At a length of 25 mm. the first dorsal is almost completely black, and there are prominent dark bars and spots symmetrically arranged on either side of the middorsal line on the body and head.

The three specimens sexed, 22 to 25 mm. in standard length, proved to be nearly ripe females. If adult males are represented among the types, they show no striking external differences.

The species has been taken only once. This was from a poison station run in a small, semi-protected cove in which a vertical, alga-covered ledge dropped vertically to a uniform sand bottom 3 to 10 feet below. *Pogonymus pogognathus* was the most abundant species taken. Whether the individuals were living on the ledge or in the sand below (as seems more probable judging from the fringed lip) was not verified at the time. Just how this habitat differed from that of innumerable other poison stations run from ledges dropping off to a sand bottom remains unknown to the author.

Pogon = (Gr.) bearded; gnathos = (Gr.) jaw.

Suborder SCHINDLERIOIDEI

The two known species of *Schindleria* (see Fig. 5) were first described as members of the genus *Hemiramphus* in the 1930's. They have been bounced about from order to order ever since. The members of the genus are neotenic

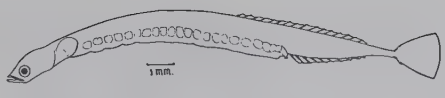

FIG. 5. *Schindleria praematurus*, female with eggs. (After Bruun.)

fishes, apparently without close relatives, which have lost the adult characteristics that would presumably indicate their relationships. The present erection of a new suborder of perciform fishes for *Schindleria* is not made on the basis of any decisive new material; it merely seems to be the best available solution to a difficult problem. Knowledge of *Schindleria* may be marshaled under four heads: neoteny, sexual differentiation, soft anatomy, and "osteology." These will be dealt with only in so far as they bear on the systematic position of the genus.

Neoteny: That a 20 mm. *Schindleria* may be sexually mature is often indicated by the conspicuous presence of large eggs in the females. That the rest of the fish is in a larval stage of development is shown by the presence of the atrium directly behind, i.e., on the same horizontal plane with, the ventricle (Schindler, 1932: pl. 4c); by what is apparently a functional pronephros (Schindler, 1932: 25); by the well-developed opercular gill (Schindler, 1932: 12); the tremendous, protruding eyes; the rounded pectoral fin attached to a lobate, fleshy base; the transparent body; and by the degree and nature of the "ossification" of the skeleton (see below).

Neoteny in fishes is rare, and nowhere is it carried to the extreme found in *Schindleria*. It is also apparently sporadic, occurring as it does in some of the Clupeiformes (e.g., Salangidae), in at least one member of the Beloniformes (*Cololabis adocetus*), and perhaps in the gobioid Perciformes. Consequently, its neotenous nature is of no great aid in the systematic placement of *Schindleria*. One is merely inclined to ask the irrelevant question why neoteny does not occur more often among fishes of the open ocean.

Sexual Differentiation: Aside from the primary sex organs there is in the males (but not the females) of *Schindleria*, especially in *S. praematurus*, a long urogenital papilla (Schindler, 1932: 6, 8; Bruun, 1940: 7, fig. 2). In addition, the anus of both species lies farther back along the body in females than in males (Schindler, 1932: 6, 8; Bruun, 1940: 5).

Soft Anatomy: In 1932 Schindler described the soft parts of *Schindleria praematurus* with special reference to the heart, swim-bladder, gills, and the digestive and urogenital systems. None of the features described, nor the sexual differentiation, provides the present author with any clue as to the taxonomic relationships of the genus.

"Osteology": There is some difficulty in determining what should be included under "osteology." Schindler (1932: 6) states: "An ossification or deposit of lime in the vertebrae is not present." However, the vertebrae take up alizarin stain. In the account of the osteology that follows all those portions that stain with alizarin will be considered "ossifications."

As the final comment in his paper on *Schindleria*, Giltay (1934: 10) has said: "Des matériaux plus nombreux nous permettront de mieux définir ses affinités, surtout quand on aura mieux pu étudier le squellette qui est deja relativement bien développé." There are several difficulties with this proposition. First, additional material has been gathered and it has not helped much. Second, the degree of ossification in the additional specimens is about the same as in those taken earlier, and there seems little hope of finding an adult-type ossification in *Schindleria*. Third, the "ossification" that is present occurs to approximately the same extent and in about the same areas as in a larval anchovy of the same size. To what extent this larval-type ossification in *Schindleria* is comparable to the bony structure of other adult fishes is an open question. (In this author's opinion, the "ossifications" that do occur in *Schindleria* are not of an adult fish type at all but are merely calcifications of normally larval structures. Indeed, it seems that the adult *Schindleria* has retained larval features which have to some extent "ossified" precociously as compared to the ontogenetic development of the same features in normal fishes. If this is true, the calcifications in *Schindleria* bear little comparison with normal adult fishes and are only incompletely comparable with any larval stage.)

Judging from the absorbtion of alizarin stain, the jaws, vertebral centra, and fin rays are the best ossified portions of *Schindleria*. The upper jaw consists of a toothed premaxillary and a toothless maxillary of about equal length (Fig. 6a). The premaxillary has an upwardly projecting flange a little more than halfway out. The premaxillary pedicel is broad and low, articulating medially with a large cartilaginous (?) median pad and laterally with the maxillary. The latter bone has an abrupt, sharp-angled bend (Fig. 6b) that hooks around the premaxillary pedicel; the bone then projects medially inside the pedicel.

The lower jaw consists, so far as can be determined, of a single ossification (Fig. 6e), though an obscure "suture" between dentary and articular may have been missed.

The suspensorium runs very obliquely forward in order to pass below the very large eye (Fig. 6c) between the skull and the lower jaw. The only portion of the suspensorium that takes stain is a long splint made up of the quadrate below and the hyomandibular above (Fig. 6e). From the rear of the hyomandibular projects an elongated, leaf-shaped operculum.

The hyoid apparatus (Fig. 6e) consists of a vaguely ossified glossohyal in front, an elongate ceratohyal, and an epihyal. The last bone loops around posteriorly to join the upper portion of the hyomandibular. There are 5 short branchiostegals; 2 on the ceratohyal and 3 on the epihyal. There are 4 gill arches (Schindler, 1932: 11); the lower pharyngeals are separate.

The forward portion of the cranium does not take up stain. To the rear above there are three small, partial ossifications which are here

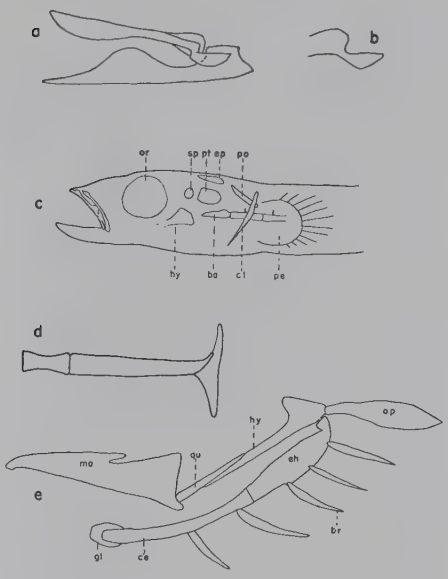

FIG. 6. *Schindleria*. a, Left premaxillary and maxillary from the inside, the posterior end of the maxillary somewhat raised. b, Median end of left maxillary from above. c, Head and fore part of body to show certain "ossifications." d, Caudal skeleton and posterior portion of "vertebral column." e, Mandible, suspensorium, opercle, and hyoid apparatus. ba, "Basioccipital"; br, branchiostegal ray; ce, ceratohyal; cl, cleithrum; eh, epihyal; ep, epiotic; gl, "glossohyal"; hy, hyomandibula; ma, mandible; op, opercle; or, orbit; pe, pectoral lobe; po, "posttemporal"; pt, pterotic; qu, quadrate; and sp, sphenotic.

provisionally identified as epiotic, sphenotic, and pterotic. Running in under the skull is a projection of the vertebral column which may represent the basioccipital (Fig. 6c); a possible alternate interpretation of this "bone" is suggested below.

The pectoral girdle consists of two simple struts (Fig. 6c) representing the cleithrum and probably the posttemporal. There is nothing in the fleshy lobe between the cleithrum and the pectoral rays that absorbs alizarin stain.

The vertebral centra stain clearly but the neural and haemal arches seem to be represented only by short spines that ride on the centra. The number of differentiated vertebrae vary from 33 to 39 in the genus (Schindler, 1932: 6, 8). At the rear of the vertebral column is a rodlike structure with an upturned tip that runs for the length of about 3 normal vertebrae. To its posterolateral face is attached a plate (Fig. 6d). Both of these features take stain well.

Since it is this terminal portion of the axial skeleton that forms the feature of *Schindleria* unique among all known fishes, some discussion of it seems in order. The terminal plate would appear to take the place of the hypural fan, differing from the usual caudal skeleton in the complete lack of separate ossifications. The rodlike portion of the "vertebral column" ahead of it is difficult to interpret satisfactorily. When the vertebral column first ossifies in an anchovy, the caudal portion of the column forms early as a number of small elements which eventually fuse to a considerable extent to form the adult caudal skeleton. One presumes that the tail rod of *Schindleria* evolved in a different ontogenetic fashion. The most satisfactory explanation for it that the author can find is that it represents the posterior portion of the notochord which has been replaced by cartilage and/or bone without dividing into discrete vertebral segments.

In this connection it is necessary to revert to the skull bone that was provisionally called the basioccipital in earlier paragraphs. The alternative explanation is that it is the forward end of this same notochord which has taken up stain in the same way suggested for the posterior rod.

In the caudal fin there are 13 rays, 11 of which are branched. The interneurals and interhaemals of the dorsal and anal fins respectively bear a one-to-one relationship with the vertebrae (see Bruun, 1940, fig. 2). There are from 15 to 20 unbranched dorsal rays, and from 11 to 17 unbranched rays in the anal; the pectoral contains 15 to 17 rays (Schindler, 1932: 7, 8).

Relationships: As mentioned, *Schindleria* was first described as a neotenic *Hemiramphus*.

Giltay (1934) demonstrated the incorrectness of this allocation. *Inter alia*, *Schindleria* differs from all of the Beloniformes in the low number of branchiostegal rays, the absence of fused pharyngeals, and the one-to-one relationship between dorsal or anal fin rays and vertebrae.

A rather better case could be made for placing *Schindleria* in the Syngnathiformes or Gasterosteiformes. However, the Syngnathiformes are characterized by having the first 3 to 6 vertebrae immovably united. The lack of a tubular snout, of external bony plates, and of a soft dorsal fin with closely spaced rays argues against placing *Schindleria* in either of these orders.

Turning from negative to positive indications of relationships, there appears to be only one character in *Schindleria* which provides any clues. This is, as already noted by Giltay (1934), the one-to-one relationship between the dorsal or anal fin rays and the vertebrae. It appears that this characteristic is limited to the Perciformes, being found there in the trachinoid, ammodytoid, blennioid, and many of the gobioid fishes. However, the basal perciform stock has, like other fishes, two or three soft dorsal and anal rays (with their interneurals and interhaemals) per vertebra. Just why certain perciform groups should have a one-to-one relationship between these features remains unknown. That it is a polyphyletic development is shown by the gobioid fishes, where this relationship seems to have developed within the group itself. At least, *Ptereleotris* has the usual two or three interneurals per vertebrae whereas most of the other gobioids have only one (Gosline, 1955: 166). If the one-to-one relationship has occurred several times within the perciform fishes, could it not also occur within other orders? The best available answer to this question seems to be that it apparently has not done so.

To sum up regarding the ordinal position of *Schindleria*, the genus seems to rest most easily (or rather least uneasily) among the Perciformes. There is nothing to really invalidate such a position and there is the one-to-one fin ray to vertebra relationship to recommend it. Where *Schindleria* belongs among the Perciformes is obscure. The best that can be done is to place *Schindleria* in the neighborhood of the blennioid fishes.

The reason for raising *Schindleria* to subordinal rank (rather than placing it in the Blennioidei as Giltay, 1934, has done) lies in the rodlike terminal section of the spinal column. There seems to be nothing like it elsewhere in fishes. The author has looked through the literature on both adult and larval fishes without finding anything similar. He has discussed this precaudal rod with E. A. Ahlstrom, A. F. Bruun, and C. L. Hubbs, and wishes to thank them for their help on this matter; nevertheless, nothing resembling this rod has come to light. In the great majority of modern fishes the notochord is replaced by vertebrae. However, when this occurs the vertebral replacement runs all the way back to the caudal skeleton. The uniqueness of *Schindleria* lies in the fact that vertebral development stops short some distance before the caudal skeleton.

There is one other feature of *Schindleria* that this author has never encountered elsewhere in fishes or in the literature (although this may simply indicate a gap in the author's knowledge, especially in regard to larval fishes). In *Schindleria* the hyoid apparatus (Fig. 6) articulates with the upper head of the hyomandibular. In all the fishes the author knows, the hyoid apparatus articulates by means of the interhyal at the lower extremity of the hyomandibular.

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The Ecology of *Conus* in Hawaii

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THE ECOLOGY OF *CONUS* IN HAWAII*

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INTRODUCTION

Members of the gastropod genus *Conus* (Prosobranchia: Conidae) are among the most conspicuous invertebrates on the coral reefs and marine benches that fringe the Hawaiian Islands. At least 21 species of *Conus* are known to occur in these habitats.

Investigation of these natural populations was stimulated by the existence of such a large number of closely related species in a restricted environment. This phenomenon is not unique to *Conus*, for many other genera of marine invertebrates are also characterized by large numbers of sympatric species in tropical regions. The gastropod genera *Cypraea*, *Mitra*, and *Terebra* are represented by 30-50 species in Hawaii (Edmondson 1946). A non-molluscan example is the snapping shrimp genus *Alpheus*, represented by 30 species in Hawaii (Banner 1953). The evolution of such genera has contributed to a marked enrichment of the tropical littoral epifauna. Here the number of species approaches ten times that of temperate regions (Thorson 1956).

Although these assemblages are well-known to systematists, no previous comparative ecological studies are known to the present writer. The objective of the study reported here was to describe the ecological niches of the species, to determine the extent of isolation between ecologically similar species, and thus to elucidate the mechanisms that permit a large number of closely related species to survive and retain their identity in a narrow environment.

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This paper is the first in a projected series reporting the results of ecological observations on natural populations of *Conus* in different areas, with emphasis on the Indo-West Pacific region. The research reported here was carried out while the author was a fellow of the National Science Foundation. Financial aid was also received from the Higgins Fund and the Director's Fund, Sheffield Scientific School.

Gratitude is expressed to G. E. Hutchinson, Sterling Professor of Zoology, Yale University, for inspiration and guidance. Special thanks for the collection of material are due Dr. A. H. Banner, Mr. C. E. Cutress, Mr. R. M. Gray, Mr. E. C. Jones, Miss Alison Kay, Mr. R. A. McKinsey, Mr. C. M. Stidham, Mr. R. Sheats, and Miss Shirley Trefz. Miss Marian Adachi assisted in many phases of the work. Members of the staff of the Hawaii Marine Laboratory rendered much helpful assistance. Appreciation is expressed to Dr. J. L. Brooks, Dr. E. S. Deevey, Dr. W. D. Hartman, Dr. R. H. MacArthur, and Dr. G. A. Riley for helpful discussion and criticism of the manuscript, and to Dr. E. Mayr for examination of preliminary data. All of the algae mentioned were identified by Dr. A. J. Bernatowicz. The writer is also indebted to Mr. W. G. VanCampen for translating the paper by Takahashi (1939). Mechanical analyses of substratum samples were carried out at the Connecticut Agricultural Experiment Station, where Dr. T. Tamura, Dr. P. Waggoner, and the staff of the Department of Soils gave much assistance. The help of Mrs. Nancy Kimball in the preparation

of the figures is gratefully acknowledged. The author is especially grateful to Dr. Olga Hartman for identification of the polychaetes discussed in the section on food and feeding. Without her willing and patient attention to a collection of partly digested, fragmentary remains of polychaetes, the food analyses presented here would not have been possible.

THE GENUS *CONUS* IN HAWAII

Of 45 species of *Conus* previously reported from the Hawaiian area, 32 are known from two or more specimens collected alive and are thus considered to be valid constituents of the Hawaiian marine fauna. Ecological observations on 25 of these, listed below, will be reported in this paper. Eighteen species were collected by the writer in the subtidal coral reef (noted by *) and intertidal marine bench (noted by +) habitats to be discussed in detail below, The specific names used are those given by Kohn (1959).

Conus abbreviatus Reeve*+
Conus catus Hwass *in* Bruguière+
Conus chaldaeus (Röding)*+
Conus distans Hwass *in* Bruguière*+
Conus ebraeus Linné*+
Conus flavidus Lamarck*+
Conus imperialis Linné*
Conus leopardus (Röding)
Conus lividus Hwass *in* Bruguière*+
Conus marmoreus Linné*
Conus miles Linné*+
Conus moreleti Crosse
Conus nussatella Linné
Conus obscurus Sowerby
Conus pennaceus Born*+ (Fig. 1)
Conus pertusus Hwass *in* Bruguière
Conus pulicarius Hwass *in* Bruguière
Conus quercinus Solander
Conus rattus Hwass *in* Bruguière*+
Conus retifer Menke+
Conus sponsalis Hwass *in* Bruguière*+
Conus striatus Linné*
Conus textile Linné
Conus vexillum Gmelin*+
Conus vitulinus Hwass *in* Bruguière*

Most of the species listed are widely distributed throughout the Indo-West Pacific region. One species, *Conus abbreviatus,* is believed to be endemic to the Hawaiian archipelago. It is closely related to *Conus coronatus* Gmelin, which occurs in other areas of the central and western Pacific.

Conus nanus Broderip is here regarded as conspecific with *C. sponsalis,* but the Hawaiian populations probably constitute a valid subspecies. All specimens of *C. marmoreus* known from Hawaii agree with the description of *C. bandanus* Hwass *in* Bruguière. Most systematists consider the latter a variety of *C. marmoreus,* but the Hawaiian populations probably constitute a valid subspecies.

THE HABITAT OF *CONUS*

Marine benthic communities may be separated into two principal types, "those that tolerate or require exposure to the atmosphere and occupy stable and usually hard substrata exposed to the full force of the air with each important fall of tide," and "those that do not tolerate exposure to the atmosphere and are practically always submerged in water" (Clements & Shelford 1939: 323).

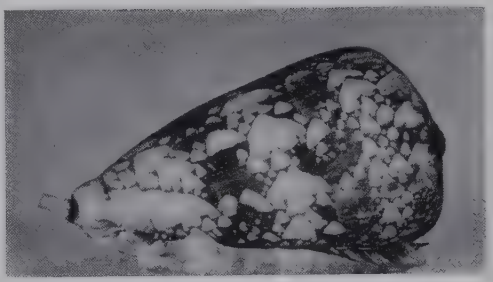


FIG. 1. Photograph of *Conus pennaceus* Born. Length of shell about 35 mm. Photograph by C. E. Cutress.

The present paper deals primarily with the ecology of natural populations of *Conus* which occupy habitats of these two types, marine benches and coral reef platforms, respectively. Notes on species occupying other habitats will also be included.

THE MARINE BENCH HABITAT

The geomorphology of emerged marine benches in the Hawaiian Islands has been discussed in detail by Wentworth (1938, 1939). These benches result from the single or combined action of processes designated by Wentworth as solution benching, water-level weathering, ramp abrasion, and wave quarrying.

SOLUTION BENCHES

In the Hawaiian Islands, solution benches occur where the shoreline is composed of reef rock and calcareous sandstone. On Oahu, this type of shore comprises 52 miles, or 31% of the coastline (Wentworth 1938). A detailed description of the characteristics and formation of solution benches is given by Wentworth (1939). A typical shore profile is shown in Fig. 2A.

Unbroken units of bench are ordinarily a few hundred feet long and 5-70 ft in width. The bench platforms are very flat. "The normal bench surface commonly shows variations of elevation of not over three to six inches in an area fifty feet wide by one hundred feet in length." (Wentworth 1939.) The outer edge of the solution bench rises more or less steeply from the water. The bench surface is ordinarily a few inches to 3 ft above mean sea level, and there is no raised rampart at the seaward margin. The bench itself is usually reef limestone, which consists of the firmly lithified skeletons of coral and calcareous algae. On the sloping outer edge, calcareous algae and, to a lesser extent, corals, contribute active building of the bench out from shore.

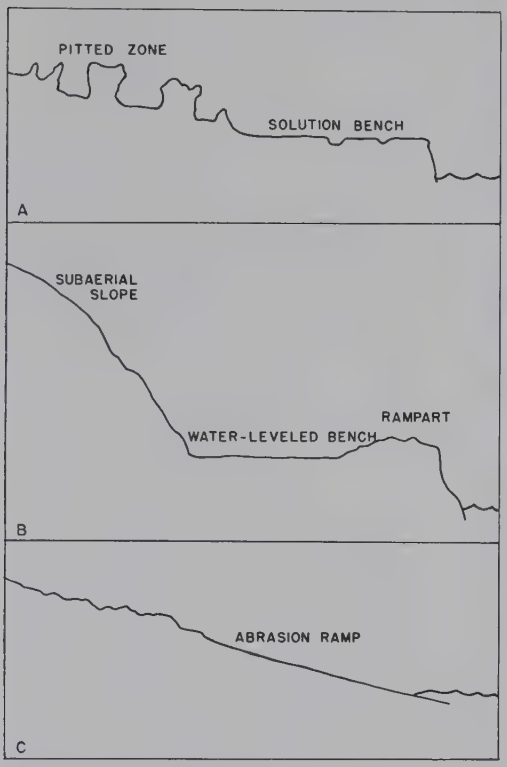


FIG. 2. Profiles of Hawaiian marine benches. A. solution bench. B. Water-leveled bench. C. Abrasion ramp bench. Modified from Wentworth (1938, 1939).

Other organisms, chiefly echinoids, are a destructive force in the same region.

The shoreward edge of the bench is sharply delimited by the front of a zone of pitted limestone (Fig. 3), ordinarily 10-50 ft in width and rising to a height of one to several ft above the bench surface. Wentworth (1939) presents evidence to show that this type of bench is formed chiefly by dissolution of the shoreward zone of pitted limestone by rain water, which collects in its pools; wave quarrying may finally produce the flat surface.

Details of solution benches selected for study are as follows:

Kahuku, Oahu (Sta. 5). The solution bench at Kahuku (Figs. 3, 4) is typical of the formation and was thoroughly investigated. It extends for several hundred feet along shore and is 40-80 ft wide. The bench surface is about one foot above mean sea level and is completely exposed for periods of up to four hours at tides of +0.2 feet[1] or less when seas are fairly calm. The coast here is exposed, and trade winds are ordinarily quite strong (about force 5). At high tide, the bench is strongly awash, and observations on it are not possible. The bench platform,

[1] All tidal data are referred to O datum = mean lower low water and are from Coast and Geodetic Survey Tide Tables.

FIG. 3. Photograph of solution bench at Kahuku, Oahu (Station 5). The width of the bench (left to right) is about 60 ft. The seaward margin of the zone of pitted limestone is visible at the left.

which is of solid reef limestone with a few potholes, is covered by a well developed algal turf. Zonation of algae across the bench is present. The landward portion is characterized by *Laurencia* sp., *Sargassum polyphyllum* J. Agardh, and *Microdictyon setchellianum* Howe; the central portion, by *S. polyphyllum, S. echinocarpum* J. Agardh, and *Halimeda discoidea*, Decaisne; and the seaward portion, by *S. echinocarpum, H. discoidea* and *Dictyosphaeria cavernosa* (Forskål) Børgesen. *Lyngbya majuscula* Harvey ex Gomont and *Cladophoropsis membranacea* (C. Agardh) Børgesen are also of common occurrence.

Nanakuli, Oahu (Sta. 11). On the leeward coast of Oahu, a limestone shore with solution benches extends, with interruptions, from Nanakuli Beach to the northern end of Nanakuli town, near Maile Head (Fig. 4). The bench is generally 50 ft or less wide, although at the end of one section it is about 100 ft. This is a very short section, however, and the bench there occupies less than one-half acre. The bench platform is about one foot above sea level, but it is less often exposed than is the bench at Station 5, described above. This is due to a prevailing heavy swell in the region, so that even at low tide large waves breaking over the bench may make collecting impossible. The algal turf is as well developed here as at Station 5. *Valonia aegagropila* C. Agardh is the dominant species. *Jania capillacea* Harvey, *Sargassum* sp., and *Padina* sp. are common. Zonation of algae was not studied, but it was not obvious.

Gastropods other than *Conus* common on solution benches are *Mitra litterata* Lamarck, *Haminoea aperta Pease,* and *Cypraea caputserpentis* Linné. A number of sea anemones are abundant. The most conspicuous Crustacea are xanthid crabs, snapping shrimp, and hermit crabs. The microfauna is especially rich. Prominent are amphipods, isopods, harpacticoid copepods, polychaetes, and Foraminifera.

WATER-LEVELED BENCHES

A formation typical of palagonite tuff and weathered basalt shores in Hawaii is the water-leveled bench, the characteristics and origin of which are dis-

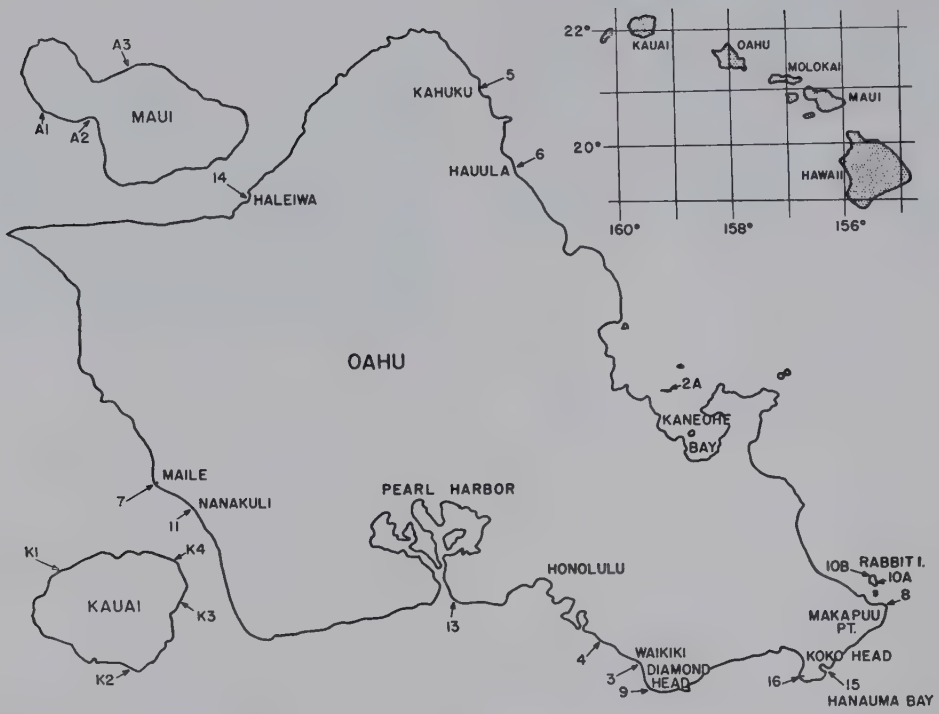


FIG. 4. Maps of the Hawaiian Islands showing location of stations. Stations lacking locality data on maps are: 2A, Sand (Ahuolaka) Island; 4, Ala Moana; 13, Ft. Kamehameha; A1, Olowalu; A2, Maalaea Bay; A3, Lower Paia; K1, Milolii; K2, Poipu; K3, Kapaa; K4, Moloaa.

cussed in detail by Wentworth (1938). Benches of this type may be 10-12 ft above sea level on exposed coasts, but are only 2-3 ft above sea level in sheltered places. Most of them are less than 100 ft wide. A steep subaerial slope landward of the bench is characteristic (Fig. 2B).

Unlike the solution bench, water-leveled benches are characterized by a well-developed rampart (Fig. 2B) of slightly higher rock at the seaward edge. The outer face of this zone is a steep cliff, characteristically occupied by echinoids. Landward of the rampart is the water-leveled bench proper. Its surface may be quite smooth or bear vertical irregularities of the order of a few inches to a foot. These are often due to differences in hardness of the dipping beds of tuff on which this type of bench is most often found.

Water-leveled benches which were given special study were as follows:

Lower Paia, Maui (Sta. A3). A fairly typical water-leveled bench near Lower Paia, Maui (Figs. 4, 5) was visited on 5 August 1956. The shore profile at this station is similar to that shown in Fig. 2B. The seaward face of the rampart zone is steep. The rampart zone (Fig. 5) averages about 15 ft wide. Its surface is irregular and is covered by a luxuriant algal turf, composed of many species. The water-

FIG. 5. Photograph of water-leveled bench at Lower Paia, Maui (Station A3) from subaerial slope. The 100-sq ft quadrat is outlined. Tide pools and rampart are also visible.

leveled part of the bench (Figs. 2B, 5) is about 15 ft wide and quite smooth. It bears a low algal turf which binds some sand. The tide was extremely low (−0.2 ft) during the period of observation, and this region was quite dry. Landward of it are large tide pools 1-2 ft deep (Fig. 5).

Milolii, Kauai (Sta. K1). Two broad marine

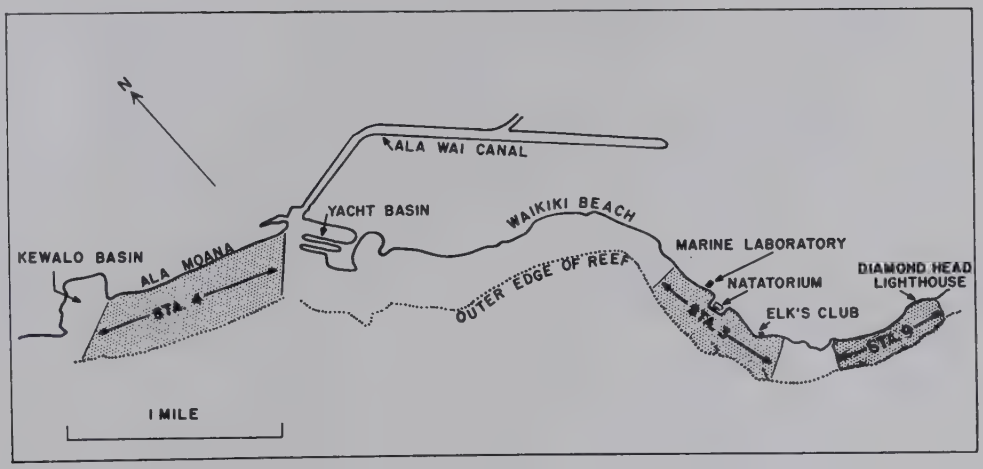


FIG. 6. Outline map of the south shore of Oahu, showing the nearly continuous fringing reef, Stations 3, 4, and 9, and landmarks.

benches fringe the shore at each end of a small beach, just east of Milolii Valley on the Napali (north) coast of the island of Kauai (Fig. 4). This region is accessible only from the sea. Four days were spent in the area in August 1955. The surface of the bench studied is about one foot above mean sea level. At minus tides it is completely exposed to the air. The benches reach a maximum width of about 200 ft. The algal turf of the platform is very low and does not present a "healthy" appearance. The dominant species is *Wurdemannia miniata* (Lamarck and DeCandolle) Feldmann and Hamel. Other species observed were *Dictyosphaeria* sp., probably young *D. cavernosa* (Forskål) Børgesen, *Gelidiella* sp., *Jania capillacea,* and *Valonia aegagropila.* At about 110 ft from shore a low pink encrusting alga, probably *Porolithon* sp., is present, and it continues to the seaward edge. The differences in flora between Station K1 and the solution benches may be due to the absence of heavy surf over most of the former.

ABRASION RAMP BENCHES

The distribution and formation of abrasion ramp benches on Hawaiian shores has not been treated in detail, but Wentworth (1938) includes a photograph of one. The formation is found on limestone and/or tuff shores. Abrasion is caused by washing of sand and gravel back and forth across the bench by waves. The result is a rather smooth sloping surface extending from below the low tide line often to several feet above it (Fig. 2C). A dense but low algal mat, usually of a varied flora, is typically present. Abrasion ramp benches are limited in size and constitute only a minor portion of shorelines. Three such benches were visited, Station 10A, on the southern shore of Rabbit (Manana) Island; Station 16, near Kawaihoa Point, on the eastern end of Maunalua Bay, Oahu; and Station A2, west of Kihei on Maalaea Bay, Maui (Fig. 3).

THE SUBTIDAL CORAL REEF PLATFORM HABITAT

More than half of the shoreline of Oahu and comparable portions of some of the other Hawaiian Islands are fringed by rather narrow coral reefs. These reefs are characterized by a predominantly sandy substratum. Living coral, patches of bare limestone and coral rubble also comprise varying proportions of the substratum, but the most actively growing corals and coralline algae are typically found at the outer edges and on the reef slopes. The reef platforms are typically subtidal and variable in depth, being usually 2-10 ft below mean sea level. Occasionally portions of the reef platform are exposed at low spring tides. The platform of some reefs is raised at the outer edge, but this rampart is often not well developed. A general discussion of Hawaiian coral reefs is given by McCaughey (1918). A typical reef fringes the south shore of Oahu, interrupted only by dredged channels and the drainage of streams. Investigation was concentrated on sections of this reef near the laboratory, noted as Stations 3 and 9 (Fig. 6). Additional collections were made at Station 4.

Brief descriptions of Stations 9 and 3, based on field notes, follow. They emphasize, respectively, the characteristics of the reef normal to the shore and parallel to the shore. The ecological notes on *Conus* which are included will serve as an introduction to the quantitative data presented below.

Diamond Head, Oahu (Sta. 9). The fringing reef on the Honolulu side of Diamond Head may be roughly divided into four zones. Zone (1) is an intertidal area of moderate surf which breaks over a substratum of detrital limestone. Landward of this zone, above the high tide limit, is a narrow sand beach. A dense growth of many species of algae occurs in zone (1), except in the bare limestone surge channels and tidal pools. This region takes the form of an abrasion ramp bench, 30-50 ft wide, which

slopes to seaward. No *Conus* were observed here, but this is perhaps due to the convenience of the area to shell collectors.

Zone (2) comprises the broad submerged reef platform, 2-6 ft below 0 tide datum. The substratum is characterized by areas of coral rubble, coral heads and sand, more or less intermingled. This region comprises most of the width of the reef, which reaches a maximum of about 1,500 ft. The areas with substratum of coral rubble are extensive. Conspicuous benthic algae are absent. These areas are also barren of large gastropods, probably because of lack of shelter provided by the pieces of rubble, which are readily moved back and forth by wave action. Scattered coral heads, usually bearing only a small colony of living coral, harbor a variety of invertebrates, including *Conus pennaceus* on the sand beneath. *C. rattus* and *C. imperialis* are occasionally epifaunal on dead coral. Sandy areas interspersed with reef limestone outcrops form the typical habitat of *Conus flavidus* and *C. lividus*, which are usually epifaunal. *C. abbreviatus* is also found, usually burrowing in sand in these areas.

Zone (3), which is variable in width, is characterized by large areas of dead coral reef, which appear to be eroding. The surface areas of these regions are often near the 0 tide datum and hence are often dry at low tide. At high tide, surf over these areas is heavy. *Conus rattus* is occasionally found, and *C. ebraeus* sometimes occurs on the vertical edges of the eroding coral areas, or in small crevices of sand below. Channels 4-6 ft deep and normal to the shore separate these areas near the outer edge of the reef and broaden into extensive areas with sand substratum just inshore. *Conus pulicarius* is found typically beneath the surface of the sand. Reef fishes abound about the steep edges.

Zone (4) is the zone of heavy surf at the outer edge of the reef, where coral flourishes. Environmental conditions precluded extensive observations.

The most common alga at Station 9 was *Lyngbya majuscula*. *Sargassum, Hypnea, Codium,* and others were also common.

Waikiki, Oahu (Sta. 3). The wide fringing reef at Station 3 appeared to offer a wide variety of microhabitats. The collecting area extended about 1,000 ft north, and about 2,500 ft south, from the Waikiki Branch of the Hawaii Marine Laboratory (Fig. 6). The width of the reef is about 600-1,000 ft. Inshore areas of the southern portion, to about the Elks Club, are characterized by more or less abundant coral rocks set in sand or sand-rubble substratum. *Conus lividus* and *C. flavidus* are often common. *C. abbreviatus* sometimes occurs in the larger sandy areas between coral rocks. Much of the reef area to seaward is eroding dead coral reef, as at Station 9, and *Conus* is generally absent. At the seaward edge of the reef are sandy areas, with some limestone outcrops. The reef slope is gentle and quite sandy. Although the area appears suitable, *Conus* occurs only occasionally. This area can be visited only on calm days, and the usually heavy surf may make this portion of the habitat unsuitable for the snails. *C. flavidus* and *C. distans* have been found however. The latter typically occurs at reef edges and generally in rougher water than the other species of *Conus*.

From the Elks Club (Fig. 6) to just north of the laboratory, the substratum is quite different. An inner reef, shoreward of a dredged channel, is limestone bench and rubble and devoid of *Conus*. The outer reef is generally deeper, being 3-8 ft below MLLW. Sand is the dominant substratum, but coral heads are abundant and there are some rubble areas. *C. lividus, C. flavidus,* and *C. ebraeus* occur but are rather sparse. *C. distans* is sometimes found at the outer edge.

The northern portion of the area sampled supported a richer fauna. The substratum was of coral heads and rocks, reef limestone, and rubble areas. A detailed discussion of this region was given by Edmondson (1928). *Conus pennaceus* occurred under rocks in sand. Epifaunal species included *C. rattus, C. flavidus, C. lividus, C. ebraeus,* and *C. abbreviatus,* none of which was uncommon. This area especially provided sites for attachment of *Conus* egg capsules. Subsequent to the investigation, however, much of this area was dredged, and the inshore portion covered by a sand beach, to create an area for swimming.

Other reefs studied were essentially similar to the two described. Helfrich & Kohn (1955) and Kohn & Helfrich (1957) discussed the characteristics of Station K3. Extensive collecting was also carried out at reefs on Oahu at Maile (Sta. 7) and Ala Moana (Sta. 4). The location of the more important reef stations is shown in Fig. 4.

LIFE HISTORY OF *CONUS*

An account of spawning and larval development of *Conus* in Hawaii is in preparation and will be published elsewhere. Therefore, only information of ecological importance will be presented here.

Spawning Site and Season

Egg capsules of at least 12 species of *Conus* have been collected in Hawaii, chiefly by Ostergaard (1950) and by the writer and colleagues.

Coral reef platforms, but not marine benches, provide suitable attachment sites for egg capsules of *Conus*. Of 36 egg masses collected in the field, 29 were recorded from reef platforms. An almost complete absence of records from marine bench habitats suggests that spawning is unsuccessful there. This is probably due to the absence of protected pools in which egg capsules may be deposited without being subject to desiccation at low tide and/or torn away by heavy surf at high tide. Recruitment of bench populations is probably from pelagic veliger larvae which have been carried from other areas and are washed onto marine benches in condition to settle and assume the benthic mode of life.

All of the capsules were found between the months of February and August, although search for them was not confined to, or emphasized during, this

period. The data suggest that most species of *Conus* spawn during about the same part of the year. The spawning season of most species for which more than one egg mass has been collected is rather extended over the period between the months cited. The most complete data are for *C. pennaceus,* of which 12 egg masses were collected, all in the months of May, June, July and August. The data are probably sufficient to establish the breeding season as continuing through these months.

Reproduction and Larval Development

As is typical in the Prosobranchia, the sexes are separate in *Conus.* The male possesses an extensible penis. Copulation was not observed. In spawning, eggs are released from the genital aperture and pass ventrally over the foot in a temporary groove to the prominent aperture of the nidamental gland on the sole. There the capsular material is extruded, enclosing a number of eggs. The capsule is attached to a hard substratum, typically under a coral rock, or to the underside of the rock itself. Illustrations of the egg capsules of *Conus* are given by Ostergaard (1950). A number of capsules (3-78, in 12 species studied) are deposited to form a cluster. The number of eggs per capsule varied from 40 to 11,400 in 5 species studied.

In 4 species studied (*C. vitulinus, C. abbreviatus, C. imperialis, C. quercinus*), the trochophore stage is entered at 2-6 days, and the veliger stage at 6-10 days, after spawning. Larvae hatch as veligers about two weeks after spawning. These observations are in agreement with those of Ostergaard (1950), who also reported development of 4 other species, which hatched 12-16 days after spawning. Almost all of the eggs in a capsule develop completely, and no nurse eggs were observed.

With the exception of one species, the length of the pelagic stage could not be determined. The maximum survival time of free-swimming veligers in the writer's laboratory was 9 days. Metamorphosis was observed only in *Conus pennaceus,* which has an extremely short free-swimming stage of less than one day. On the second day after hatching, metamorphosis is virtually completed and the young snail begins to craw about on its foot. These juveniles survived for periods of up to 20 days, but no significant growth was observed after hatching. The nature of the food at this stage is unknown. Protozoa abounded in the cultures. Thorson (1946) concluded that all prosobranch larvae known from the Oresund feed on phytoplankton, and he calculated the theoretical maximum diameter of the food to be 5-45μ. The mouths of *Conus* veligers measured were of about the same diameter as the esophagus of the smaller larvae measured by Thorson. Thus the larvae of *Conus* probably depend for food on phytoplankton, nannoplankton and detritus. Examination of squash preparations of *C. pennaceus* a few days after settling revealed the presence of radula teeth. These differ in form from the adult teeth, being shorter in proportion to the thickness, and they are probably not functional. Thus neither the method of feeding nor the food is known at this stage of the life history.

Post-Larval Development and Growth

It was possible to study post-larval development only in *Conus pennaceus.* At hatching, the larvae of this species are several times as large as those of other species, measuring about 1.3 mm in shell length.

A rough estimate of the rate of post-larval growth was obtained in the following manner. Four clusters of egg capsules of *Conus pennaceus* were collected in a large tide pool adjacent to Station 9 on 13 August 1955, and additional clusters were observed but not removed. Adults collected at the same time ranged from 33 to 37 mm in shell length. On 30 November, 3.5 months later, 8 specimens of *C. pennaceus* were collected in the same tide pool. Of these, 6 were probably hatched from egg capsules the previous summer (Fig. 7). On 27 December, 41 specimens of *C. pennaceus* were collected in this tide pool.

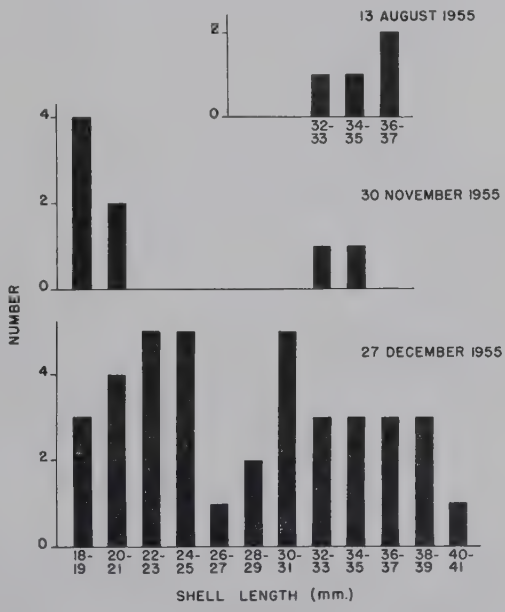


FIG. 7. Length-frequency distribution of *Conus pennaceus* at Station 9, 13 August-27 December 1955.

The length-frequency distribution of the December population is also shown in Fig. 7. Although bimodality suggesting two age classes is evident, it is quite possible that all of the specimens were spawned the previous summer. The minimum at 26-27 mm may not indicate separation of two age classes, because of the large number of specimens of greater length collected. If these were older specimens, most of them probably would have been collected from the tide pool on previous occasions. As noted above, the breeding season is long. The mean shell length of

first age-class individuals in November was 19 mm, with S.D. = 6.3 mm. In December, mean shell length was 28 mm, with S.D. = 7.7 mm. The mean mean growth rate was thus 5-6 mm/month during the first 3.5 months. During the next month the mean increment was 5 mm.

It was not possible to obtain any other growth data of this type, since such isolated populations are exceptional. Shells of a number of specimens of *Conus ebraeus, C. abbreviatus,* and *C. sponsalis* from a marine bench (Sta. 5) were marked with a diamond point vibrator and returned to their natural habitat. Of these, three specimens, all *C. ebraeus,* were recovered after 133-221 days following release. The growth increments ranged from 0.3-0.6 mm shell length and 0.2-0.4 g wet weight per month. Although only these data are available, they presumably give the correct order of magnitude of growth of older individuals.

If the growth rates cited hold for other species, it may be concluded that, in species comparable in size to *Conus pennaceus* and *G. ebraeus* (Fig. 9), several millimeters per month in shell length are added during the first few months, the rate later falling off to a few tenths of a millimeter per month.

ABUNDANCE AND POPULATION DENSITY OF *CONUS*

Darwin (1859: 319) pointed out that most species of animals are characterized by being rather rare. Since species of *Conus* are not exceptions, and because time available for collecting was limited, several of the less abundant species are represented by rather small samples. In order to determine the ecological relationships of the species, the data presented in this report have therefore been subjected to appropriate statistical analyses.

As MacArthur (1957) has shown, the expected abundance of the rth rarest species in the community of a single habitat which has been adequately sampled, and in which ecological niches are nonoverlapping and continuous, is

$$\left(\frac{m}{n}\right) \sum_{i=1}^{r} \left(\frac{1}{n-i+1}\right) \qquad (1)$$

where m = the total number of individuals, n = the number of species, and i = the species rank. All of the data on abundance of *Conus* have been presented in comparison with the distribution expected according to this theory.

THE MARINE BENCH HABITAT

Solution Benches. The population of *Conus* at Station 5 was the densest stable population studied on Oahu. Eight species were collected, of which *C. ebraeus* was the most abundant. In 61 quantitatively sampled 100-sq ft quadrats, four species were collected. The relative abundance of species is shown in Fig. 8. If only data from the quantitatively sampled areas are included (Fig. 8A) a homogeneous population or single community is indicated by agreement

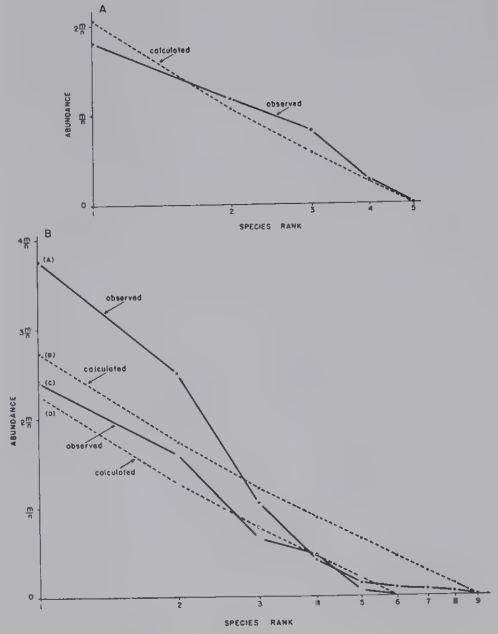


FIG. 8. Abundance of species of *Conus* at Station 5. A. Data from quantitatively sampled quadrats. m = 136, n = 4. Species rank: 1 = *ebraeus,* 2 = *abbreviatus,* 3 = *sponsalis,* 4 = *chaldaeus.*
B. Curves (A) and (B), data from all collections at Station 5. m = 500, n = 8. Curves (C) and (D), data from all collections, but with exclusion of three species characteristic of other habitats. Explanation in text. m = 484, n = 5. Species rank: (A) and (B) 1 = *ebraeus,* 2 = *abbreviatus,* 3 = *sponsalis,* 4 = *chaldaeus,* 5 = *lividus,* 6 = *flavidus,* 7 = *rattus,* 8 = *pennaceus;* (C) and (D) 1 = *ebraeus,* 2 = *abbreviatus,* 3 = *sponsalis,* 4 = *chaldaeus,* 5 = *rattus.*

of the observed curve with the expected distribution for the community of a uniform habitat.

Curve (A) in Fig. 8B is based on summation of results of all 18 collecting trips made to Station 5. The slope is steep, since common species are too common and rare species too rare. The curve is therefore not in good agreement with the theoretical distribution (Curve B), and a heterogeneous population, or the inclusion of occupants of more than one habitat, is indicated. The heterogeneous aspect of the total population may be explained as follows: Three of the species included occur more typically in habitats other than the solution bench platform. All three, *Conus pennaceus, C. flavidus,* and *C. lividus,* are typically subtidal species, which are rarely exposed by receding tide, and they occur much more commonly where such a habitat is provided, as will be shown below. If the abundance curve is plotted without these species, the resulting line (C) is considerably straighter and approaches the theoretical curve (D) more closely. It is therefore apparent

that the sparse occurrence of three species which are more typical residents of a different habitat contributes to the heterogeneity shown by the curve (A) for total abundance at Station 5.

The mean density of *Conus* on this bench is 2.2 individuals/100 sq ft, based on the 61 quantitatively sampled quadrats. The mean population density of species censused in quadrats is shown in Table 1A.

TABLE 1. Population Density of Species of *Conus* at Two Marine Bench Stations.

Species	Mean number per 100 sq. ft. (=9.3m.²)
A. Station 5	
Conus ebraeus	1.02
Conus abbreviatus	0.66
Conus sponsalis	0.41
Conus chaldaeus	0.15
	2.24
B. Station K1	
Conus abbreviatus	0.85
Conus ebraeus	0.55
Conus sponsalis	0.48
Conus catus	0.24
Conus chaldaeus	0.18
Conus rattus	0.09
Conus flavidus	0.03
Conus retifer	0.03
	2.44

The mean biomass of all species was calculated to be about 0.6 g dry organic matter/100 sq ft, or 0.065 g/m².

The species differ in size. Length-frequency distributions are shown in Fig. 9. The population is essentially an adult one, and juvenile specimens are rarely found. Despite numerous collecting trips at all times of year, no egg capsules of *Conus* were ever found.

At Station 11, nine species of *Conus* were collected, of which *C. sponsalis* was the most abundant. In eight 100-sq ft quadrats, quantitatively sampled in September, four species were present, with mean density of 5.5 individuals/100 sq ft and abundances as shown in Fig. 10. The curve shows that the observed number of *C. sponsalis* (38) is much higher than that expected in a homogeneous population containing the observed numbers of the other species.

An even denser population was observed on 29 November 1955. At this time, counts of two areas, each of but one sq ft, were 3 and 7 individuals of *Conus sponsalis*. No other species were present. This abundance (= 500/100 sq ft) was present only on the extremely wide area of bench described above.

This high density of *Conus sponsalis* is believed to be related to the fact that the individuals were much smaller (mean length 13.5 mm) than elsewhere (mean length 22.1 mm at Sta. 5). Length-frequency distributions of specimens collected at Station 11 in September and November are shown in Fig. 11A. The September population is unimodal. However, the

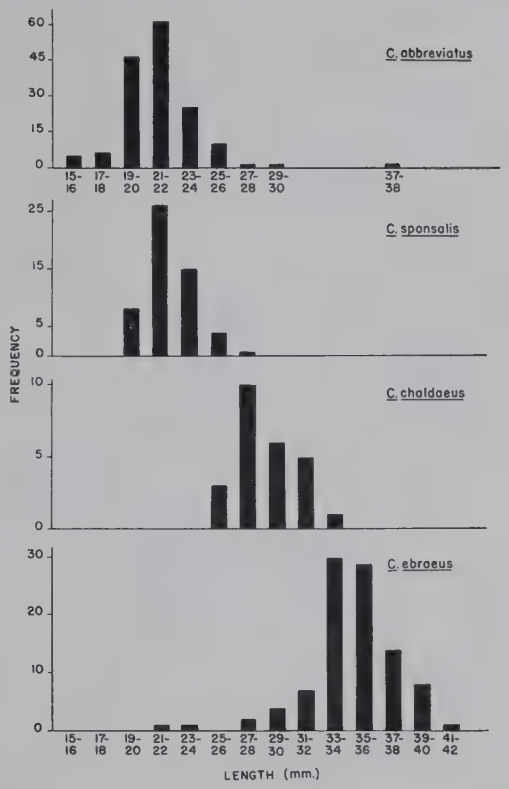


FIG. 9. Length-frequency histograms of the dominant species of *Conus* at Station 5.

November population is bimodal, with an absence of individuals of 12-13 mm. This suggests that a new age class of 6-11 mm individuals has been added to the population. Unfortunately, no information is available on the reproductive cycle of *C. sponsalis*. However, egg capsules of many species of *Conus* are found in summer and if eggs were laid in August, hatching might take place in September, with settling of pelagic veliger larvae in October giving rise to a dense population of juvenile individuals in November. Although no egg capsules were found at Station 11, the bench is interrupted by rather deep, somewhat protected pools, which may provide suitable spawning sites. Alternatively, larvae may arrive in numbers from other areas in settling condition.

Population density varied greatly in the area of Station 11. Particularly densely populated sections were quantitatively sampled by the transect method. In these regions, two transects of eight quadrats gave the mean density of 5.5 individuals (of four species)/100 sq ft. The maximum observed density of about 500 juveniles/100 sq ft has been mentioned.

On other occasions, searches of 0.63 and 1.25 man-hrs resulted in only one and three specimens, respectively. Since the time required to sample a 100-sq ft quadrat was usually 5 minutes (0.08 hr), this

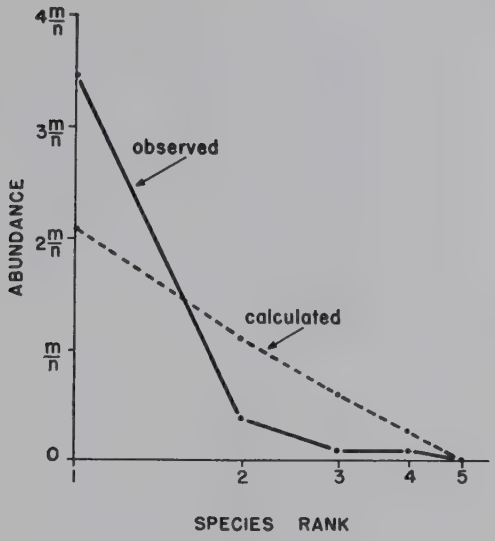
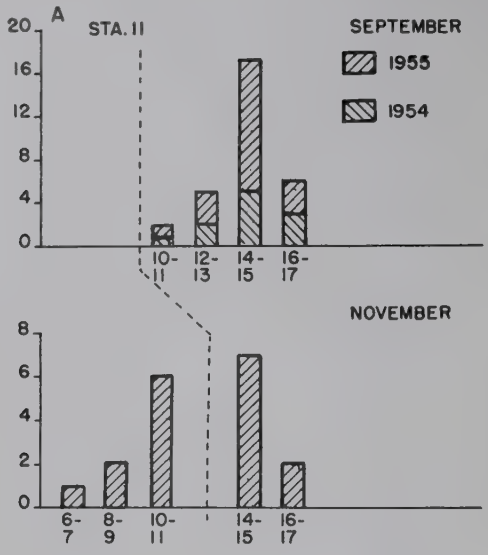


FIG. 10. Abundance of species of *Conus* at Station 11. Data from quantitatively sampled quadrats. m = 44, n = 4. Species rank: 1 = *sponsalis*, 2 = *chaldaeus*, 3 = *ebraeus*, 4 = *rattus*.



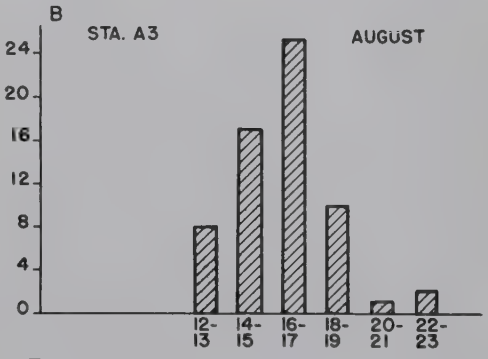


FIG 11. Length-frequency histograms of *Conus sponsalis*. A, Station 11. B, Station A3.

factor can be used to convert time-relative to space-relative density. A search of 0.63 man-hr would thus cover 7,900 sq ft and 1.25 man-hrs 15,600 sq ft. Corresponding densities are 0.01 and 0.02 individuals/100 sq ft, respectively.

Water-leveled Benches. Six species of *Conus* were collected at Station A3, of which *C. sponsalis* was by far the most abundant. The abundance of species is plotted in Fig. 12. Fig. 12A represents total abundance, and 12B the abundance in a single quantitatively sampled 100-sq ft quadrat on the water-leveled part of the bench (Fig. 4). Both curves show an obvious inflection point, which is caused by the relatively great abundance of *C. sponsalis*. Disagreement with the calculated theoretical distribution suggests a heterogeneous population.

Density on the water-leveled bench at Station A3 was second only to that in the two 1-sq ft quadrats sampled at Station 11. At Station A3, only the single quadrat was sampled. However, this represented a considerable fraction of the total available area (Fig. 4). One specimen of *Conus flavidus* and 25 *C. sponsalis* were present in this area.

The length-frequency distribution of *Conus sponsalis* at Station A3 is unimodal (Fig. 11B). The population is probably an adult one, although the individuals are not as large as those at Station 5. The relative superabundance of *C. sponsalis* cannot therefore be ascribed to an influx of first age class juveniles. Since the observations were made on 5 August, during the probable spawning season, this is even less likely.

Marine benches do not in general provide suitable sites for deposition of egg capsules of *Conus*. However, a specimen of *C. catus* was collected at Station A3 in spawning condition, as evidenced by the deposition of an egg capsule which was attached to the shell after collection.

Station K1. At Station K1, all *Conus* present in 33 quadrats, each of 100 sq ft, were counted. Eight species were present in the area sampled, of which the most abundant was *C. abbreviatus*. Relative abundance of species is shown in Fig. 13. The distribution calculated from Equation (1) is also included, and the data are seen to be in excellent agreement with it. This supports the observation that the habitat is a rather uniform one, with a homogeneous population, or single community, of *Conus*.

The solution bench at Station 5 was the only area

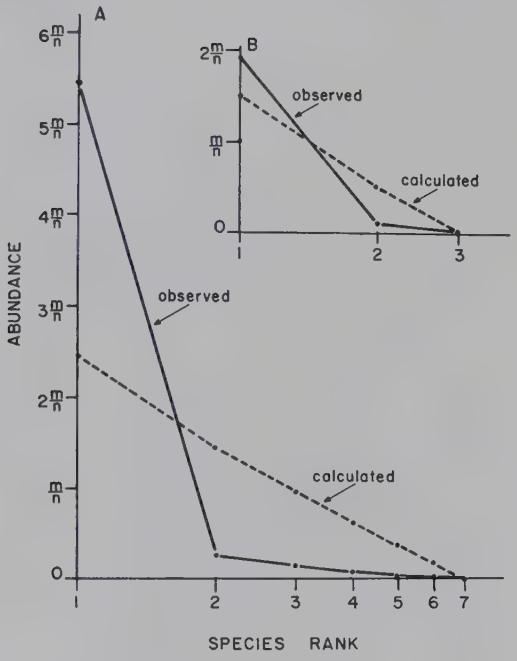


FIG. 12. Abundance of species of *Conus* at Station A3. A, Total data. m = 166, n = 6. B, Data from quantitatively sampled quadrat. m = 26, n = 2. Species rank: A. 1 = *sponsalis*, 2 = *rattus*, 3 = *catus*, 4 = *flavidus*, 5 = *abbreviatus*, 6 = *chaldaeus;* B. 1 = *sponsalis*, 2 = *flavidus*.

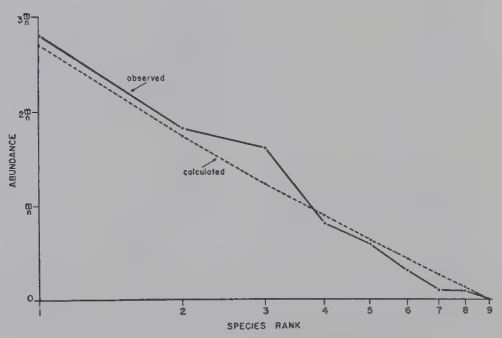


FIG. 13. Abundance of species of *Conus* at Station K1. Data from quantitatively sampled quadrats. m = 81, n = 8. Species rank: 1 = *abbreviatus*, 2 = *ebraeus*, 3 = *sponsalis*, 4 = *catus*, 5 = *chaldaeus*, 6 = *rattus*, 7 = *flavidus*, 8 = *retifer*.

sampled more intensively than Station K1. The three most abundant species are the same at the two sites, although the order is different. The mean density of all *Conus* species at Sta. K1 is 2.44 individuals/100 sq ft, based on the 33 quantitatively sampled quadrats. The mean density of each species is shown in Table 1B. The mean density of *C. abbreviatus* is higher, while that of *C. ebraeus* is lower, than at Station 5. The densities of *C. sponsalis* and *C. chaldaeus* are about the same at the two stations.

Abrasion Ramp Benches. The rather smooth sloping surface and attendant wave action of abrasion ramp benches provide a rather unfavorable habitat for large gastropods. However, some shallow crevices provide shelter at high tide. A total of but 47 specimens of seven species of *Conus* were collected in five field trips to abrasion ramp benches. On all such benches studied, *C. rattus* was the most abundant species. *C. sponsalis* and *C. abbreviatus* were relatively common, and *C. chaldaeus, C. flavidus,* and *C. lividus* were also present.

SUMMARY

Data on abundance and population density of *Conus* on all marine benches studied are summarized in Table 4. Between six and nine species are found in such habitats. However, the figures in the fourth column of Table 2 probably indicate the number of species comprising a homogeneous population, at least at the more thoroughly studied stations. On very narrow water-leveled and solution benches, *C. sponsalis* is the dominant species, and only 1-3 other species may be present. Wider benches are occupied by proportionally greater numbers of species. As will be shown below, the species are then distributed non-randomly across the bench platform from shore to seaward edge.

TABLE 2. Summary of Abundance and Population Density of *Conus* on Marine Benches

Station	Width of Bench (ft.)	Total Number of Species	Number of Species in Quadrats	Number of Quadrats Sampled	Density (No./100 sq. ft.)	Most Abundant Species
Solution Bench Stations						
5	60	8	4	61	2.24	*ebraeus*
11	40	9	4	8	5.5 (0.01*-500)	*sponsalis*
Water-leveled Bench Stations						
K1	200	9	8	33	2.44	*abbreviatus*
A3	15	6	2	1	26	*sponsalis*
Abrasion Ramp Bench Stations						
Total	...	6	..	0	1.0*	*rattus*

*Calculated from time-relative density.

The species of greatest abundance is variable among benches of similar, as well as different, geological origin. Abrasion ramp benches were not studied in detail, hence data from them are combined in Table 2. However, *Conus rattus* was the most abundant species at all three such benches visited, and it may be termed typical of this formation. This species was of minor importance on both solution benches and water-leveled benches.

Sampling of a large number of 100-sq ft quadrats at Stations 5 and K1 indicated that a fairly stable population of 2-2.5 individuals/100 sq ft may be ex-

pected on solution benches and water-leveled benches. Other areas sampled quantitatively were those in which extremely large populations were observed by inspection. Conversion of time-relative to space relative density suggests a lower limit of population density on marine benches of about 0.01 individual/100 sq ft.

The Sub-tidal Reef Platform Habitat

Inspection of a number of coral reef platforms led to the conclusion that the abundance and distribution of *Conus* in these habitats are characterized by patchiness. This not unexpected phenomenon must be considered in interpreting the data presented in this section and in the following one on distribution.

In Figs. 14-17, data on abundance at the four thoroughly sampled reef stations are presented. No one species is most abundant on all of the reefs. At each station, however, either *Conus flavidus* or *C. lividus*, or both, represent one or both of the two most abundant species. This is in marked contrast to marine bench stations where, as has been shown above, these two species occur infrequently.

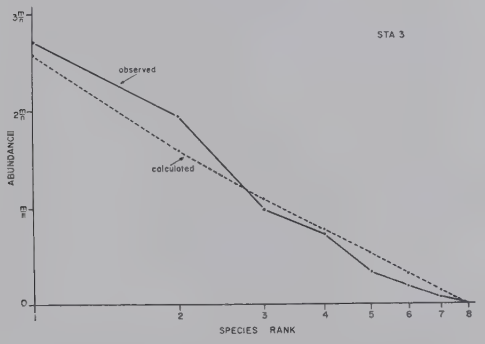


FIG. 14. Abundance of species of *Conus* at Station 3. m = 182, n = 9. Species rank: 1 = *flavidus*, 2 = *lividus*, 3 = *ebraeus*, 4 = *abbreviatus*, 5 = *rattus*, 6 = *imperialis*, 7 = *striatus*.

At only one of the adequately studied reef stations is the most abundant species neither *Conus lividus* nor *C. flavidus*. At Station 7, the most abundant species was *C. sponsalis*. This is attributed to substratum factors, which will be discussed in detail below.

At all stations, agreement of the results of analysis of abundance data with the curve calculated from Equation (1) is sufficient to justify the conclusion that the subtidal reef platform constitutes a single rather than composite habitat, which supports a homogeneous community or interspecific population of *Conus*. The striking agreement of the observed and calculated curves for Station 7, which is the closest of any census thus far analyzed in this manner (MacArthur, personal communication), is probably fortuitous.

Population Density. Population density of *Conus* was more difficult to study directly on subtidal reef

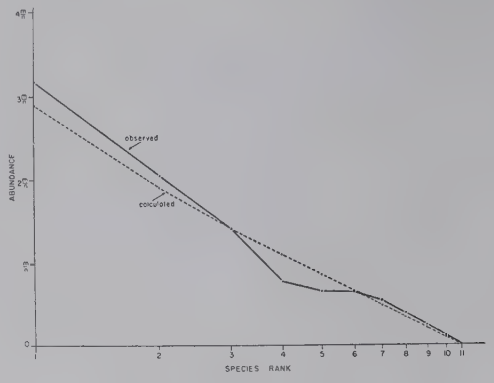


FIG. 15. Abundance of species of *Conus* at Station 4. m = 78, n = 10. Species rank: 1 = *lividus*, 2 = *flavidus*, 3 = *abbreviatus*, 4 = *imperialis*, 5 = *ebraeus*, 6 = *rattus*, 7 = *vitulinus*, 8 = *sponsalis*, 9 = *chaldaeus*, 10 = *vexillum*.

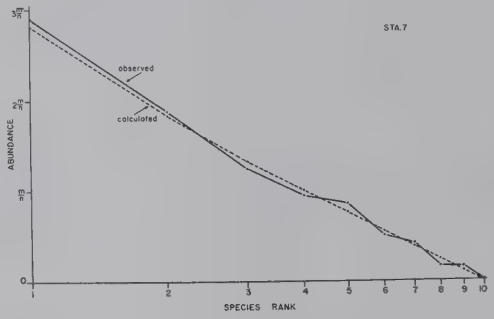


FIG. 16. Abundance of species of *Conus* at Station 7. m = 182, n = 9. Species rank: 1 = *sponsalis*, 2 = *lividus*, 3 = *ebraeus*, 4 = *flavidus*, 5 = *pennaceus*, 6 = *abbreviatus*, 7 = *rattus*, 8 = *distans*, 9 = *chaldaeus*.

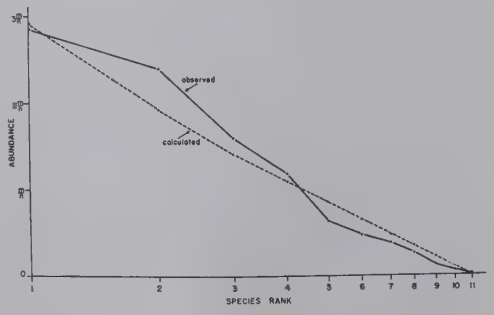


Fig. 17. Abundance of species of *Conus* at Station 9. m = 187, n = 10. Species rank: 1 = *flavidus*, 2 = *pennaceus*, 3 = *lividus*, 4 = *abbreviatus*, 5 = *pulicarius*, 6 = *ebraeus*, 7 = *imperialis*, 8 = *vexillum*, 9 = *rattus*, 10 = *marmoreus*.

platforms than on marine benches. This was due both to technical difficulties and to the obvious patchiness of the populations. During most field trips,

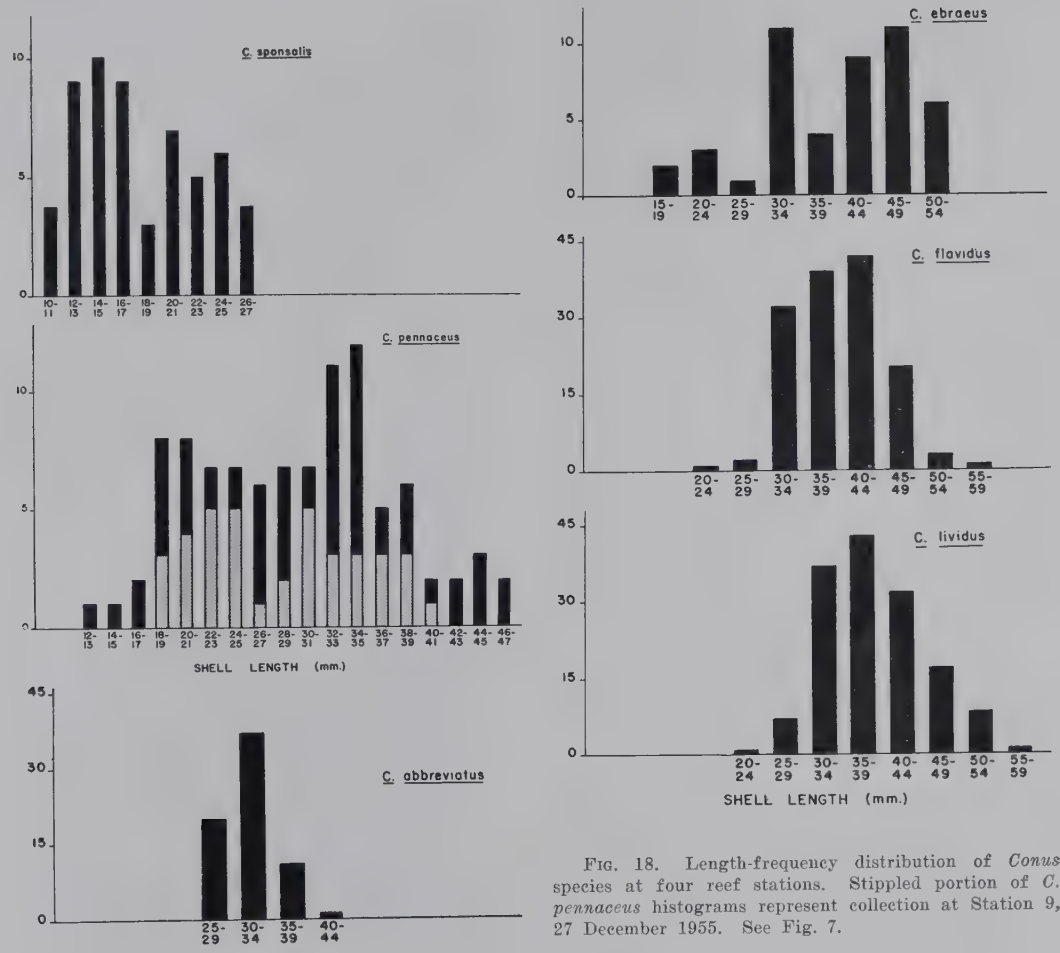


FIG. 18. Length-frequency distribution of *Conus* species at four reef stations. Stippled portion of *C. pennaceus* histograms represent collection at Station 9, 27 December 1955. See Fig. 7.

collecting efforts were of necessity concentrated in areas of greatest abundance. Conversion of time-relative to space-relative density would thus give values considerably in excess of the mean density on the entire reef platform.

At one reef station (Sta. K3, see Helfrich & Kohn 1955) transects of known area were sampled quantitatively. The results (Table 3) show that the mean population density of all species in the area sampled was 0.16 individual/100 sq ft. This is lower by an order of magnitude than the density on marine benches. This relationship is probably generally valid, although favorable parts of reef platforms may support local populations which approach those of marine benches in density.

The mean biomass of *Conus* in the quantitatively sampled areas at Station K3 was calculated to be 0.06 g dry weight organic matter/100 sq ft (0.0065 g/m^2). Although the population density on marine benches is about 15 times as large as on reef platforms, the biomass of *Conus* is only ten times as great. Although the comparisons are extremely rough, the discrepancy is probably real. Comparison of Figs. 9 and 18 clearly shows the prevalence of larger individuals in the populations occupying reef habitats. The mean shell length of two species common in both habitats is compared in Table 4. These values are 13% and 54% larger in reef platform than in marine

TABLE 3. Population Density of *Conus* at Station K3.

Area Sampled (sq. ft.)	Species	Density (No./100 sq. ft. =9.3 m.^{2})
3,000	*C. ebraeus*	0.07
	C. abbreviatus	0.07
	C. chaldaeus	0.03
	C. flavidus	0.03
		0.20
3,000	*C. ebraeus*	0.10
1,200	*C.* (species not noted)	0.17

Mean Density of All Species=0.16

bench populations of *C. ebraeus* and *C. abbreviatus*, respectively. This may reflect the more equable environmental characteristics of the former habitat. The mean shell length of *C. sponsalis* on reefs was 17.8 mm. In bench populations, mean shell length ranged from 13 to 22 mm. The explanation may be that *C. sponsalis* occupies those parts of reef platforms where conditions most closely approximate those of marine benches.

TABLE 4. Mean Shell Length of Reef and Bench Populations of *Conus ebraeus* and *C. abbreviatus*.

	Length in Millimeters			
	All Reefs		Sta. 5 (bench)	
	Mean	S.D.	Mean	S.D.
C. ebraeus...	39.0	9.7	34.6	3.2
C. abbreviatus	32.7	3.1	21.3	3.5

Except for the growth studies reported above, collection data were not analyzed for seasonal variations, since observations were made only during a single complete annual cycle.

Community Diversity and Heterogeneity

The similarity of the species composition of different populations may be conveniently measured by an index of diversity given by Koch (1957):

$$I = \frac{t-n}{n(P-1)} \qquad (2)$$

where n = the total number of species represented, P = the number of populations or communities sampled, and t = the arithmetic sum of n_1, n_2, n_3, ... n_p, which are the numbers of species in each population or community. If I is low, the species composition differs greatly from population to population. I approaches unity with increasing similarity of the populations compared.

This index was calculated separately for the four most thoroughly sampled reef stations (Sta. 3, 4, 7, and 9) and the four most thoroughly sampled bench stations (Sta. 5, 11, K1, and A3). In both cases, I was 0.58. Comparison of total collections from all bench stations with those from all reef stations gave I = 0.61. The three indices are so similar that there would appear to be no greater ecological difference between the reef and bench habitats than among different reefs, or among different benches. This is misleading, however, since the index used measures only similarity of qualitative species composition.

Consideration of quantitative data concerning the relative abundance of species in different habitats suggests a different interpretation. It has been shown that individual reefs and benches generally support homogeneous populations of *Conus* (Figs. 8, 10, 12-17). Inspection of these graphs shows that three species, *C. sponsalis*, *C. ebraeus*, and *C. abbreviatus*, are rather consistently the most abundant species on marine benches, while two entirely different species, *C. lividus* and *C. flavidus*, are dominant at almost every reef station.

A comparison of the relative abundance of all species at all reef and bench stations is shown in Fig. 19. Of the 18 species considered, 6 are proportionally more abundant on marine benches than on reef platforms. In 4, the discrepancy in abundance between the two types of habitats is at least one order of magnitude. Twelve species are relatively more abundant on reefs than on benches. The discrepancy is at least one order of magnitude in 8 of these.

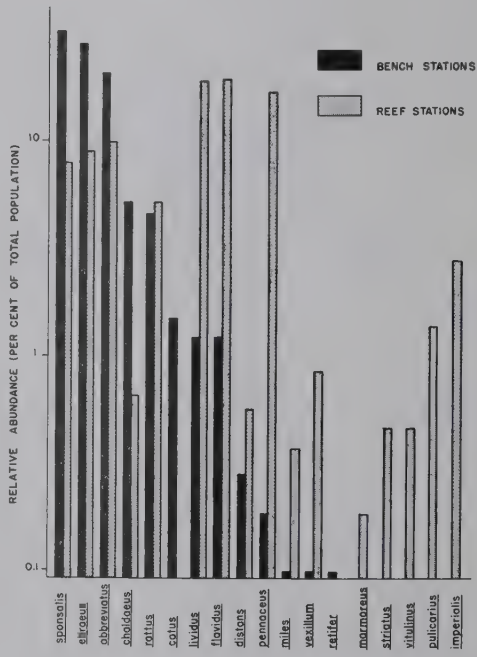


FIG. 19. Relative abundance of *Conus* species at all bench stations (solid histograms) and all reef stations (stippled histograms).

A more quantitative measure of community heterogeneity, H', based on information theory, is given in Equation (3), which is modified from Margalef (1956):

$$H' = I_{m(AB)} - \left(\frac{I_{m(A)} + I_{m(B)}}{2}\right) \qquad (3)$$

in which

$$I_m = \frac{1}{m} \log \frac{m!}{m_1! \cdot m_2! \cdot \ldots \cdot m_s!} \qquad (4)$$

where m = the number of individuals of all species, m_1 = the number of individuals of the most abundant species, and m_s the number of the rarest species. The subscripts are equivalent to the values on the abscissas of Figs. 8, 10, and 12-17 and the values can be determined from data given in the graphs.

In Equation (3), A and B signify different communities. Equation (3) can be expanded for application to more than two communities. Equation (5) gives H′ for four communities, A, B, C, and D:

$$H' = I_{m(ABCD)} - \left(\frac{I_{m(A)} + I_{m(B)} + I_{m(C)} + I_{m(D)}}{4} \right) \quad (5)$$

sampled bench stations (Figs. 8, 10, 12, 13), H′ = 0.19.

Application of Equation (3) to summations of abundances at the four most thoroughly sampled reef stations (combined as community "A") and the four most thoroughly sampled bench stations (combined as community "B") gave H′ = 0.84.

The low heterogeneity of the *Conus* communities at individual stations has been demonstrated above. In addition, a low value resulted when the measure of heterogeneity introduced by Margalef (1956) was calculated for summed abundance data from four reef stations. Calculation from summed data from four benches gave a similar low value. However, comparison of summed data from four reefs with summed data from four benches resulted in a high value, indicating marked heterogeneity between the communities of *Conus* in these two kinds of habitats.

To summarize, two types of habitats, reef platforms and marine benches, were distinguished on the basis of observational data presented in the previous section. The data reported in the present section are interpreted as justifying this separation by indicating its significance to the gastropods under consideration, as well as to the investigator.

LOCAL DISTRIBUTION OF *CONUS*

Marine Benches

Distribution of *Conus* across bench platforms was studied by the transect method. Two parallel lines, marked at 10-ft intervals and 10 ft apart, were secured across the bench from inshore edge to near the seaward margin. Ten-foot square areas of the platform were thus delimited. In each transect series, all of the *Conus* visible in each 100-sq ft area were counted. Counts were made at night, when the gastropods were actively crawling about on the bench. For convenience, it was assumed that all of the snails in the study areas were visible from above and none were buried in the algal turf or under stones or coral, as is often the case in the daytime.

Solution Benches. Distribution of *Conus* species, based on data from transects made at Station 5, is shown graphically in Fig. 20. Only the four most abundant species at Station 5 were observed in the transects. The populations of these species are not randomly distributed across the bench platform from pitted zone to outer edge. Interspecific differences are apparent from Fig. 20. Although *C. abbreviatus* is the more abundant, it and *C. sponsalis* are similarly distributed (Wilcoxon test: P ≫ .05). Most of the populations of these two species occupy a strip within 20 ft of shore, independently of the width of the bench. In contrast, the peak density of *C.*

Application of Equation (5) to the abundance data presented (Figs. 14-17) for populations of *Conus* at the four most thoroughly sampled reef stations gave H′ = 0.09. For the four most thoroughly

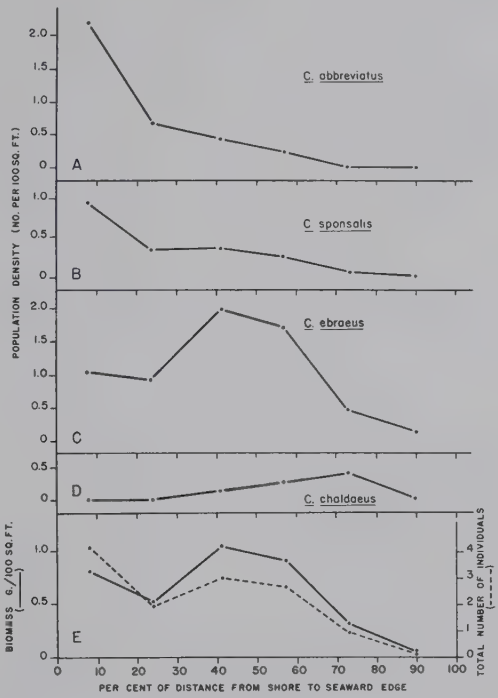


FIG. 20. Distribution of species of *Conus* across bench at Station 5. Each point to the left of 90% represents the average of 8 or 9 transects. The points at 90% represent the average of 5 transects. If width of bench varied from 60 ft at transect site, data were adjusted to a width of 60 ft.

ebraeus occurs about halfway across the bench. Lower densities occur near shore and near the outer edge. The density peak of the least abundant species, *C. chaldaeus,* is nearer the outer edge, but the edge itself is not occupied. This species rarely occurs in the shoreward zone occupied by *C. abbreviatus* and *C. sponsalis.* Wilcoxon tests showed that the distribution of *C. ebraeus* differs significantly from that of *C. sponsalis* (P< .05) and from that of *C. chaldaeus* (P< .01).

The biological significance of this pattern of distribution will be discussed below. The total density of all species of *Conus* tends to decrease toward the outer edge. Fig. 20E shows this distribution in density as well as in terms of dry weight, excluding shells.

At Station 11, the distribution of *Conus sponsalis* across the bench is shown in Fig. 21 to be essentially similar to that at Station 5. Most of the population

occupies the more protected shoreward portion of the bench. The striking difference between the populations at Stations 5 and 11 is the virtual absence of *C. ebraeus* and *C. abbreviatus* at the latter (Fig. 10), although the type of habitat afforded seems suited to these species.

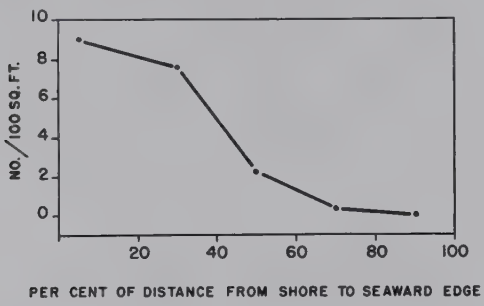


FIG. 21. Distribution of *Conus sponsalis* across bench at Station 11. Data from transects.

Water-leveled Benches. The patterns of distribution across the bench at Station K1, as determined by transecting (Fig. 22), are also quite similar to those at Station 5. As at Station 5, the distribution of *Conus sponsalis* and *C. abbreviatus* are not significantly different from each other ($P \gg .05$). The distribution of *C. ebraeus* differs significantly from that of *C. sponsalis* ($P < .01$) as well as from that of *C. chaldaeus* ($P < .01$).

A striking difference between the distribution patterns at Stations 5 and K1 is that although the bench at Station K1 is three times as broad as Station 5, the four dominant species occur in bands which are only about twice as wide as those at Station 5. Since population density is similar, the density peaks of *C. abbreviatus* and *C. sponsalis* are therefore considerably higher at Station K1 (5.8 and 3.5, respectively) than at Station 5 (2.3 and 0.9, respectively). Thus, in contrast with Station 5, a broad area of bench platform is present which is occupied only by *C. chaldaeus* of the four dominant species under consideration.

In this region, four other species were found. The most abundant was *Conus catus*. Densities of the others, *C. rattus, C. flavidus,* and *C. retifer,* were very low. Thus three of the species characteristic of the solution bench habitat do not extend to the seaward portion of the broad water-leveled bench at Sta. K1 but are replaced there by four other species, only one of which is common.

The density distribution of all species is shown in Fig. 22G. The density peak is relatively nearer shore than at Station 5. Total density decreases toward the seaward edge at both stations.

Station A3. Search of the rampart zone at Sta. A3 revealed no specimens of *Conus*. In addition to *Morula tuberculata,* which is the dominant gastropod, the only other common large gastropod was *Mitra*

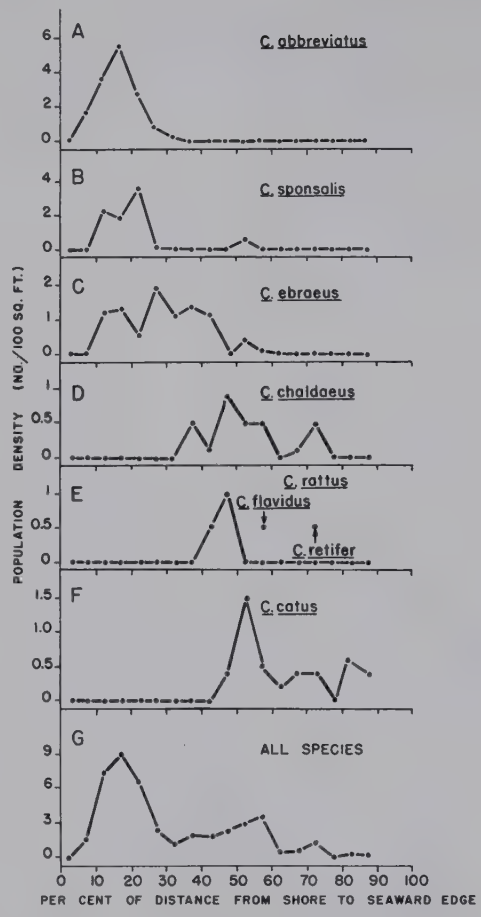


FIG. 22. Distribution of species of *Conus* across bench at Station K1. Data represent the average of two transects.

litterata. The factor which excludes *Conus* from this microhabitat is not known. Almost all of the specimens of *Conus sponsalis* were collected on the flat water-leveled platform. They were found with the shells partly buried in the algae-sand turf, and they thus apparently avoid desiccation during the day. The other species, in contrast, were found more typically on the inner margin of the rampart and level bench platform, or in other sites where the irregular tuff provides shelter during the day. These species may be too large to obtain adequate protection from the thin algal mat. The heterogeneity shown by the abundance curve (Fig. 12) can be accounted for by these microhabitat differences. It is of interest that the single specimen of *C. flavidus* collected in the quadrat was only 13 mm long, less than one-half the normal adult length of this species.

REEF PLATFORMS

The most apparent characteristic of the distribution of *Conus* on reef platforms, patchiness, has been mentioned above. It is believed to be related primarily to the nature of the substratum, discussed in more detail in the following section.

Technical difficulties and low population density on reef platforms precluded the use of the transect method for determining patterns of distribution normal to the shoreline. The less exact method of noting the approximate site of individual specimens, in terms of per cent of the distance from shore t outer edge where the specimen was collected, was employed. These data were recorded in the field by the method described by Kohn (1956a). In this manner the approximate distribution of 274 specimens of 11 species at four reef stations was determined. Most of the data concerned five species at three stations, as shown in Table 5. Data for Station 7 are tabulated separately. At the other stations, samples were somewhat biased since collecting effort was greater on the inshore half of the reef than the offshore half. At Station 7, the effort was not so biased, and the similarity with data from the other stations suggests that the latter are valid. The evidence thus indicates that more intensive collecting on the offshore parts of other reefs would reveal *Conus* in low density, and this was confirmed by inspection.

TABLE 5. Distribution of Five Species of *Conus* Across Reef Platforms at Stations 3, 7, and 9.

Per cent of Distance From Shore to Outer Edge	*abbreviatus*		*flavidus*		*lividus*		*ebraeus*		*sponsalis*		Total
Sta.	7	T	7	T	7	T	7	T	7	T	
0- 30	4	8	6	26	12	23	7	10	2	2	69
30- 60	0	4	6	16	10	18	2	10	20	20	68
60- 90	3	3	3	5	4	5	7	8	29	29	50
90-100	1	2	0	0	3	4	1	2	2	2	10
	8	17	15	47	29	50	17	30	53	53	197

T=Stations 3+7+9

The distribution patterns normal to the shore of *Conus abbreviatus, C. flavidus, C. lividus,* and *C. ebraeus* do not differ significantly from each other in the samples observed ($P > .05$). The distribution of *C. sponsalis* at Station 7 may differ significantly ($P > .05$) from that of *C. ebraeus* and thus from those of all other species. This variation, however, is in the opposite direction from that observed on marine benches, where *C. sponsalis* characteristically occupies the shoreward zone (Figs. 20-22). On the subtidal reef platform at Station 7, the bulk of the population of this species occupies the central region of the reef (Table 5). This is probably due to the infrequency of suitable substratum nearer shore, as will be discussed below.

The distribution patterns of *Conus lividus* and *C. flavidus,* two closely related species which are also similar in size, are strikingly similar, but some of the predominance of inshore individuals may be due to sampling bias.

The total density of all species is similar over most of the reef platform from shore to outer edge (Table 5). The total density decreases as the breaker line is approached, but sampling bias is also in this direction. The downward trend in the first three figures in the right hand column of Table 5 is probably not significant.

It may be concluded, then, that over most of the area of reef platforms the distribution of *Conus* is patchy, or clumped, and is not related to distance from shore or breaker line. In the zone of surf and very close to shore, however, *Conus* is less abundant, although present in low density.

SUBSTRATUM

MARINE BENCHES

By definition, a habitat must possess uniformity with respect to an important quality (Andrewartha & Birch 1954: 28). In the case of marine benches, uniformity is in the physiography of the bench platform, which constitutes the substratum of the species under consideration. This substratum is hard, rather smooth, and covered with an algal turf which may vary markedly in density. The algae, if sufficiently dense, bind sand, which is of importance because its presence increases the amount of residual water retained on the bench at low tide, and because it provides a medium into which *Conus* may burrow in order to escape desiccation or heavy wave action.

The substratum is of importance not only to adult *Conus,* but also to the pelagic veliger larvae. The importance of certain attributes of the substratum in the settling of pelagic larvae of certain other benthic marine invertebrates has been demonstrated by Wilson (1952, 1955), and this is likely to be the case in *Conus* also. Peculiarities of the substratum of marine benches may attract larvae of some species and not of others and thus determine qualitatively the species composition of the population of this habitat. The possibility of obtaining direct evidence relevant to this hypothesis was remote. However, it is probably one of a number of density-inactive mechanisms (Nicholson 1955) which determine the specific composition of populations of *Conus* on marine benches.

The hypothesis that the microhabitats of different species differed with respect to substratum preferred by the adults is more amenable to study. The predominant substratum of marine benches is the hard, algal-matted reef limestone noted above. In addition to the zonation of distribution discussed in the previous section, variations of substratum exist which may further differentiate microhabitats. These are patches of bare limestone or tuff which do not support an algal turf, and patches of sand, which usually fill shallow depressions in the bench platform. In the latter, benthic algae may or may not be present. The association of various species of *Conus* with these regions is summarized in Table 6A.

TABLE 6. Proportion of Populations of *Conus* Species Associated with Different Types of Substratum.

A. Marine Benches

Species	Sample Size	Bench with Algal Turf, Binding ± Sand		Sand Pockets or Patches on Bench		Bare Limestone or Turf	
		No.	%	No.	%	No.	%
C. sponsalis	211	189	90%	10	5%	11	5%
C. abbreviatus	96	63	65%	25	26%	6	6%
C. ebraeus	97	63	65%	15	15%	17	18%
C. rattus	45	28	62%	5	11%	11	24%
C. chaldaeus	29	13	45%	8	28%	8	28%
C. catus	11	5	45%	2	18%	4	36%
	489	361	74%	65	13%	57	12%

B. Reef Platforms

Species	Sample Size	Sand		Reef Limestone with or without Algal Turf		Dead Coral and Coral Rubble	
		No.	%	No.	%	No.	%
C. pulicarius	12	12	100%	0	0%	0	0%
C. abbreviatus	73	57	78%	13	18%	3	4%
C. lividus	133	86	64%	29	22%	18	14%
C. ebraeus	54	33	61%	11	20%	10	19%
C. flavidus	130	73	56%	34	26%	23	18%
C. imperialis	23	11	48%	6	26%	6	26%
C. sponsalis	61	23	38%	24	39%	14	23%
C. rattus	37	8	22%	14	38%	15	40%
	659	405	61%	160	25%	94	14%

C. *Conus pennaceus* on Reef Platforms

	Sample Size	Sand		Reef Limestone, with or without Algal Turf	Dead Coral and Coral Rubble
		Visible From Above	Under Rocks		
day	79	2	70	3	4 (all under rocks)
night	57	30	0	26	1 (visible from above)
Total	136	32 (102)	70	29	5
Per cent		75%		21%	4%

Most individuals of all species are found on the most abundant kind of substratum, algal turf on hard bench platform. A certain proportion of each species "spills over" onto the other types of substratum available. This frequency is significantly less in *Conus sponsalis* than in the other species. *C. abbreviatus* utilizes sandy areas more often than *C. sponsalis* ($P < .01$). *C. ebraeus* utilizes bare regions of bench more often than *C. abbreviatus*, but the difference is probably not significant ($P = .08$). Substratum preferences of other species do not differ significantly from one another.

The particle size distribution in samples of sand from several stations was determined by the use of graded sieves, in order to detect possible interspecific differences in preference for sand of diffrent mechanical proprties. The methods used varied but slightly from those of Holme (1954).

Since sand particles are subject to sorting by wave action, larger particles might be expected to dominate in samples taken near the outer edge of benches. Application of Wilcoxon tests to data from Stations 5 and K4 showed that *Conus ebraeus* is associated with somewhat coarser sands than *C. abbreviatus* ($P = .05$). However, mechanical properties of the sand probably do not vary sufficiently to provide different microhabitats with respect to this factor.

Sandy areas are more common on reef platforms than marine benches. The small areas of sand on benches may limit the density of some species of *Conus*. *C. pennaceus* is found rarely on benches, but it is common in habitats where sand is abundant, as the animals typically remain in sand under rocks during the day. Other species of *Conus* which occur in low densities on marine benches (e.g. *C. lividus, C. flavidus*) may be limited indirectly by the absence of sandy substrata which are required not by them but by the species on which they prey (see section on Nature of the Food of *Conus* on Marine Benches).

REEF PLATFORMS

The predominance of a sand substratum and the absence of extensive living coral characterize the platforms of Hawaiian fringing reefs and distinguish them from those of typical atoll and barrier reefs.

The nature of the substratum associated with 659 individuals of the 9 most abundant species of *Conus* on reef platforms is summarized in Table 6B. Most of the specimens (61%) of all the species collected on reef platforms occupied sandy substrata. From 12% to 14% of the populations were found on each of the other types of available substrata: bare limestone, limestone with algal turf (combined in Table 6B), and coral (including coral rubble and dead coral). The relative abundance of the available types of substratum was not measured, but sand is by far the most prevalent. Thus, as is the case on marine benches, most of the population of *Conus* occupies the most abundant type of substratum.

Specific Differences of Substratum. Conus pulicarius is probably entirely restricted to a sandy substratum. Although the sample size in Table 6B is small, it is supported by similar unpublished data from other regions where this species occurs. *C. pulicarius* typically occurs in areas of reefs characterized by sand bottom and the absence of limestone outcrops and growing coral. Individuals are usually partly or completely buried during the day. At night, they actively crawl about through the sand, leaving a broad track which is visible from above and facilitates collection. In quiet water, these tracks are often visible the next morning, and they may lead to the discovery of completely buried individuals.

Conus flavidus and *C. lividus*, the two most abundant species on reef platforms, also occur predominantly on sand substrata but are commonest in areas of sand patches and smaller pockets among solid substratum. These two species do not differ significantly from each other with respect to the types of substratum utilized ($P = .15$; see Table 20). Both species are predominantly epifaunal, and individuals are rare-

ly found even partly buried in the substratum during the day.

Conus abbreviatus is also primarily a sand dweller when it occurs on reef platforms. It will be recalled that this species also occupies sandy regions of marine benches significantly more often than do the other species present. *C. abbreviatus* also burrows in sand on reef platforms significantly more often ($P < .01$) than the other species, with the exception of *C. pulicarius*.

The proportions of different types of substratum utilized by *Conus ebraeus* on reef platforms do not differ significantly from those of the other predominantly sand-dwelling species just discussed (Table 6B). This species is also typically epifaunal, but some individuals are found partially buried in the substratum.

Conus pennaceus is also primarily associated with a sand substratum. However, in contrast to the other species, the substratum of *C. pennaceus* is altered by the diurnal activity cycle. The substratum of 79 specimens collected during the day and 57 collected at night is shown in Table 6C. During the day, specimens are characteristically found on (37%) or partly buried in (63%) sand under basalt or coral rocks. At night, the snails actively crawl about on the surface of the sand or on reef rock, and they are visible from above. The substratum of *C. pennaceus* thus differs qualitatively from those of the other sand dwellers, which are found uncommonly under rocks.

The number of specimens of *Conus sponsalis, C. imperialis,* and *C. rattus* found on other types of substratum exceeds the number found on sand. Most of the specimens of *C. sponsalis* listed in Table 6B were collected at Station 7, where it is the most abundant species of *Conus*. *C. sponsalis* occurs sparsely or not at all on the other reefs studied (Figs. 14-17). The substratum of a large area of Station 7, particularly where *C. sponsalis* is common, consists of rather smooth limestone, which supports an algal turf, and dead coral, which presents a rough surface but is apparently being smoothed by wave quarrying. The former type of substratum especially is similar to that of marine benches, where *C. sponsalis* is also abundant. It is therefore not surprising that, when such a substratum is available on an otherwise predominantly sandy reef platform, it should be occupied by a population of *C. sponsalis*. Only a few scattered individuals of *C. sponsalis* are found on reefs which lack extensive areas of this type of substratum.

Conus rattus is also found more often on lithified than on sandy substrata, and in this respect probably does not differ significantly from *C. sponsalis* ($P = .08$). The numbers of these two species found on each of the substratum-types listed in Table 6B are significantly different, however ($P = .02$), in the samples collected.

Analysis of Particulate Sediments. The five most abundant species of *Conus* on subtidal reef platforms are characteristically associated with the sand moiety of the substratum. It was therefore of interest to determine the properties of the particulate sediments and the distribution of *Conus* with respect to these properties.

The sediments are almost entirely biogenic, comprising chiefly Foraminifera tests, fragments of coral, mollusk shells, echinoid tests and spines, and calcareous algae. Small amounts of olivine are often present, especially at Station 9, located at the foot of Diamond Head (Fig. 6), which takes that name from the local term "Hawaiian diamonds" for olivine.

Sediments associated with seven species of *Conus* on reef platforms were analyzed. *C. lividus* was found to be associated with somewhat coarser sediments than *C. flavidus* (Wilcoxon test: $P = .05$). However, all species are associated with sediments with extremely variable particle size distribution in the sand-gravel range. It therefore seems likely that, on reef platforms as on marine benches, there is no niche diversification of *Conus* species with respect to the particle size distribution of the sand moiety of the substratum.

EFFECTS OF ENVIRONMENTAL STRESSES

As Prosser (1955) has recently stated, "Determination of the importance of specific variations requires (a) the careful observation of ecological niches of subspecies and species occupying overlapping habitats, and (b) physiological tests of the effects of environmental stresses."

In order to test the effects of some environmental stresses on the species of *Conus* that inhabit marine benches, experiments on the effect of strong water currents and low oxygen tension were carried out. In addition, observations on activity with respect to desiccation will also be reported. The environment of the subtidal reef platform habitats is in general more equable than that of intertidal marine benches.

Temperature

Water temperatures ranging from 22.8 to 28.3°C were recorded at marine bench stations. The extreme range is probably somewhat greater, especially in shallow pools at low tide. Seasonal fluctuations appeared to be extremely small. Sea temperatures ranging from 22.0 to 29.1°C were measured on reef platforms. More extensive data for Station 3 were published by Edmondson (1928), who reported extremes of 21.5 and 29.0°C.

Analyses of diurnal fluctuations of temperature at Station K3 have been published elsewhere (Kohn & Helfrich 1957). On successive days in summer, ranges of 24.3-29.1°C and 24.1-27.1°C were recorded. The amplitude of diurnal temperature fluctuation thus closely approaches the annual range of variation on at least some reefs.

Temperature is not a limiting factor to species tolerant of the prevailing range, and population densities do not affect, and are not affected by, temperature. The qualitative species composition of

populations of *Conus* in Hawaii may, however, be determined at least in part by the temperature regimen. The Hawaiian Islands represent the highest latitudes at which most of the species present are known to occur. The fauna of islands at lower latitudes, where sea temperatures are higher, is richer. Some species may be excluded from the Hawaiian area by temperatures below their tolerance limits. However, most regions nearer the equator which have been studied lie closer to the Indonesia-Melanesia center of distribution, and distance from this center is also a factor of major zoogeographical importance.

Exposure to Air at Low Tide

Marine benches, but not reef platforms, are subject to periodic exposure to air at times of low tide. Therefore, only a limited range of depth of water is available on marine benches at low tide, ranging from 0 (hereafter noted as "exposed") to about a foot in tidal pools.

A certain fraction of the population of each species of *Conus* was found to be left exposed at low tide, when the bench platform may not be awash for periods of up to four hours (Table 7). The frequency of exposure is significantly higher in *C. sponsalis* than in all other species ($P < .01$), mainly because the sample contains the large population at Station A3, which was entirely exposed. This dense population, and the virtual absence of *C. abbreviatus*, has been noted above. *C. abbreviatus* may be unable to withstand the long periods of exposure to air required for habitation of Station A3.

Table 7. Proportion of Populations of *Conus* Species Exposed to Air at Low Tide.

Species	Sample Size	Number Exposed	Per Cent Exposed
C. sponsalis	144	79	55%
C. abbreviatus	83	29	35%
C. chaldaeus	31	10	32%
C. ebraeus	73	21	29%
C. catus	28	8	29%
C. rattus	47	8	17%

Data from all marine bench stations.

The low proportion of the population of *Conus rattus* which is out of water at low tide is probably due to the fact that this species occurs more often on abrasion ramp benches than on other types. Since these slope into the sea, they are more often awash at low tide than the horizontal platforms of solution benches and water-leveled benches.

All species of *Conus* observed by the writer tend to remain quiescent in the daytime. On marine benches, the algae-sand turf provides shelter from heavy wave action at high tide, when the entire bench is awash, and the residual water it retains at low tide reduces the danger of desiccation for the smaller species (*C. sponsalis, C. abbreviatus*) during the day. If the turf is dense enough and sufficient sand is present, the shells may be completely buried. Larger species (*C. ebraeus, C. chaldaeus*) find shelter in shallow crevices or under pieces of coral rubble in the daytime.

In order to ascertain whether different species occupy different microhabitats with respect to depth of water at low tide, the proportion of each species population partly buried or otherwise sheltered was determined. The samples were rather small and excluded completely buried individuals. Nevertheless, the frequency of burrowing in *C. abbreviatus* is significantly greater than in any of the other species ($P < .01$). This is probably due at least in part to the preference of this species for sandier regions of the bench platform, where burrowing can be more easily accomplished. Proportions of populations of other species buried during the day did not differ significantly from each other in the samples examined.

Although seemingly unsuitable shelters that are vacant can always be found on marine benches, the density of available sheltered sites, and the ability of *Conus* to locate them when needed, may be a limiting factor of population size in some cases.

Heavy wave action, a prominent environmental factor on marine benches, is generally absent from subtidal reef platforms except near the outer edge. Large waves are broken by the outer edge of the reef, and wave action on the platform is rarely so heavy as to interfere with collecting or observation, even at high tide.

Activity Rhythms

At night, especially at low tide, the snails are typically up on the surface of marine bench platforms, moving actively about. This activity rhythm persists when *Conus* is maintained in laboratory aquaria. Degree of expansion of the foot, movement of the siphon, and movement of the entire animal are much greater at night than in the daytime, even if the aquaria are illuminated at night. Rhythmicity of activity in nature is thus probably at least partly endogenous.

Alternating periods of light and darkness are important to many marine invertebrates because they synchronize rhythms of locomotor and other activities (Brown *et al.* 1953). In the field, no interspecific differences in activity with respect to light or time of day, which might lead to reducing the possibility of interspecific competition, were noted. Enhanced activity may be correlated with the immediate presence of food, as Ohba (1952) observed in *Nassarius*, and as was shown in *Conus striatus* in the laboratory (Kohn 1956b).

The relationship of tidal fluctuation to locomotor activity in *Conus* is probably complex. Observations were hampered by the fact that most marine benches are accessible only at low tide. Maximum activity was observed during low spring tides at night. At such times, waves may not break over solution benches for periods of several hours. The retention of much residual water by the algae-sand mat and the absence

of solar radiation probably make the problem of desiccation negligible.

The initial movements of *Conus,* which begin after sunset, are mostly vertical, being directed out of the daytime hiding place up onto the bench platform. This behavior pattern is illustrated from field observations which comprised counts made in seven 100-sq ft quadrats at Station 5 at intervals over a 4-hr period in the evening. No *Conus* were visible on the bench platform at 1800 hrs, but by 2030, 17 specimens of four species had become active and were crawling about on the surface of the 700-sq ft area studied. By 2200, three additional individuals had also become active. Time of low tide (−0.2 ft) was 2023. Ohba (1952) noted activity peaks of *Nassarius* in tide pools at times when agitation of the water ceased on the receding tide and was renewed on the rising tide. In the present study, however, the bench had been exposed since before 1800. The rhythm is probably timed so that increased activity begins when two factors, darkness and absence of strongly flowing water, become favorable.

Since heavy wave action made observations on benches impossible except at low tide, experiments designed to measure the ability of *Conus* to withstand strong currents were carried out. Individuals of the four species dominant on marine benches were subjected to artificially created currents of 20, 100, 175 and 210 cm/sec. The ability to withstand the currents was found to be roughly correlated with size, in that *C. ebraeus,* which is larger than the other species (Fig. 9), is the most tenacious. The tenacity of *C. sponsalis, C. abbreviatus,* and *C. chaldaeus* is similar, although individuals of the last named species are somewhat larger (Fig. 9).

These data may offer a partial explanation of the observed pattern of distribution on solution benches (Fig. 20). The two smallest species are less able to withstand strong currents generated by waves breaking over the bench. By occurring chiefly on the landward portion, they are probably able to spend more time seeking food between high tides. The larger and heavier *Conus ebraeus,* on the other hand, being better able to withstand strong currents, may find a wider area of bench within its optimal habitat.

The ability of *Conus chaldaeus* to withstand strong currents in the experiments was comparable only to that of *C. sponsalis* and *C. abbreviatus.* In size, *C. chaldaeus* ranks between these species and *C. ebraeus* (Fig. 9). The experimental data thus do not help to explain the distribution pattern of *C. chaldaeus,* which characteristically occurs at the more seaward portion of marine benches. However, the data may suggest a possible explanation for the small population size of this species at Station 5, where wave action is more violent than at Station K1 and other collecting sites.

Reef Platforms. Diurnal activity cycles are difficult to observe on reef platforms. Most specimens were collected during the day, when they are typically quiescent. Little apparent difference in activity is observable in the field in the case of typically epifaunal species such as *Conus lividus* and *C. flavidus.* However, both of these species probably feed only at night, as will be shown below, and they are therefore presumably most active then.

Diurnal differences in the activity of *Conus pennaceus* are more readily observable, as alluded to in the previous section. This species is almost always found on or partly buried in sand under rocks during the day (Table 6C). At night, however, the snails leave that microhabitat to crawl about on the surface of the sand or on coral or limestone. Of 60 specimens of *C. pennaceus* collected at night, three were found crawling about out of water. Exposure to air is insignificant as an environmental stress on reef platforms, however. Exposed individuals of other species were found even more rarely or not at all.

Oxygen Requirements

Diurnal cycles of solar radiation and semidiurnal tidal cycles are factors leading to large fluctuations in oxygen concentration in the sea water on Hawaiian marine benches. Amplitude of fluctuation is greatest at low tide. At mid and high tides, oceanic water breaking over the bench in surf is probably always saturated. During daytime low tides residual water on the bench platform becomes supersaturated with oxygen due to photosynthesis by the dense mat of attached algae. At night low tides, oxygen content of residual water is reduced by respiration of both plants and animals.

Determinations of oxygen concentration *in situ* were made at three marine bench stations. Determinations were made by the Winkler method. The highest concentration measured was 7.68 ml 0_2/l, and the lowest was 0.97 ml 0_2/l, or only 19% of saturation.

It was thought that the nocturnal minimum might represent an environmental stress on *Conus.* In an attempt to determine the oxygen requirements of *Conus* and the ability to survive low oxygen tension, experiments on three of the four dominant species on marine benches were carried out in a simple respirometer. The results of three experiments, each with 14-20 specimens of *C. ebraeus,* and six experiments, each with 16-20 specimens of *C. chaldaeus,* are summarized in Fig. 23. Seven experiments with *C. abbreviatus* had erratic results, and they have not been included in Fig. 23. Indeed, all results were rather erratic, as indicated by the large standard errors. Some of this variation may be due to diurnal and tidal cycles in rate of respiration, such as have been reported in other gastropod genera by Sandeen, Stephens & Brown (1954).

The data in Fig. 23 suggest that *Conus ebraeus* and *C. chaldaeus* are probably physiological adjusters rather than regulators with respect to oxygen. That is, the rate of consumption varies with the environmental concentration rather than remaining relatively constant (Prosser 1955).

Three respiratory rate determinations of *Conus*

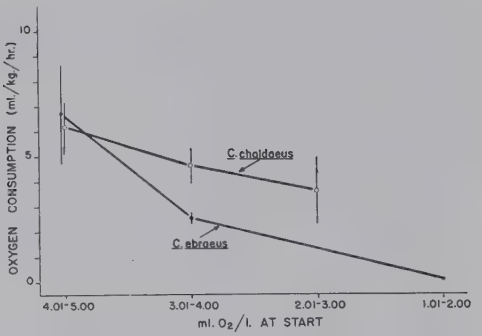


FIG. 23. Rates of oxygen consumption of *Conus* at different oxygen concentrations. Vertical lines indicate standard error of mean.

ebraeus in water containing 1.03-1.19 ml 0_2/l, near the lowest *in situ* concentration measured, showed no detectable uptake of oxygen over a period of 6 hrs. Nevertheless, all animals survived the experiment. On marine benches, oxygen concentration is probably never so low for so long a time. In addition, the typical activity cycle of *Conus* tends to obviate danger of hypoxia. When the snail crawls about out of water on the bench platform, a thin layer of water over the ctenidia ensures diffusion of oxygen from the air as the concentration in the water is reduced by passage of oxygen into the tissue.

Reef Platforms. Like temperature, oxygen concentration of the water over subtidal reef platforms undergoes diurnal fluctuation of lower amplitude than on marine benches. A graphic presentation of the diurnal cycle of oxygen concentration at Station K3 has been published (Kohn & Helfrich 1957). The minimum concentration recorded (at 0300) was 3.58 ml 0_2/l, equivalent to 77% saturation. Midday values ranged to 7.27 ml 0_2/l, or 168% saturation. A few determinations of oxygen concentration were also made at Stations 3, 7, and 9. The maximum value observed was 8.91 ml 0_2/l (197% saturation) recorded at Station 7.

Dissolved oxygen is probably never in short supply to *Conus* on reef platforms. However, individuals of several species burrow into the sand substratum. Below a centimeter or so, these sands are usually gray. This reducing environment probably does not adversely affect *Conus*, however, since the inspiratory organ, the siphon, projects above the water-sand interface and draws a stream of oxygenated water over the ctenidia.

FOOD AND FEEDING

The Feeding Process

Members of the genus *Conus* are known to have a unique feeding mechanism (discussed in detail by Bergh 1896, and Hinegardner 1957, 1958) and are known to be predatory (Alpers 1932a, Kohn 1955). The feeding process in piscivorous species has been described elsewhere (Kohn 1956b). Alpers (1932b) studied the feeding process in *C. mediterraneus* Hwass *in* Bruguière, which feeds on polychaetes. He concluded erroneously that *Conus* ejects venom into the water in the vicinity of the prey, and he was not able to discern the function of the radula teeth.

Feeding of several of the vermivorous species which occur in Hawaii was observed in the laboratory. In *Conus abbreviatus* and *C. ebraeus*, the manner of injecting the radula tooth and accompanying venom do not differ from that described (Kohn 1956b) for *C. striatus*. However, the radula tooth is not held by the proboscis after injection. Rather, the proboscis retracts quickly, leaving the tooth in the prey. The mouth then expands and the paralyzed prey is engulfed. However, as will be noted below, other vermivorous species do retain the radula tooth within the proboscis and use it to draw the impaled prey into the mouth, as does *C. striatus*.

The method of feeding is somewhat different in *Conus pennaceus*, which, as will be shown, feeds on other mollusks. When the prey is stung, the radula tooth is completely freed from the proboscis. In contrast with the vermivorous species, not one, but up to six radula teeth may be injected into the same prey organism. If the prey is an opisthobranchiate mollusk with an internal shell, it is usually swallowed whole. The shell is presumably later regurgitated, since it is usually too large to pass into the intestine. When the prey is a prosobranch, or an opisthobranch with a large external shell, the shell is not swallowed. Rather the mouth of *C. pennaceus* is applied to the aperture of the shell of the prey after stinging. This position is maintained for 15 min-1 hr, following which the shell, now empty, falls away. Presumably the venom acts on the columellar muscle during this time, relaxing its attachment to the shell and allowing the soft body to be removed intact from the shell and swallowed. The feeding process was observed to be essentially identical in *C. textile*.

Digestion. After the prey has been completely swallowed, it lies in a large, distensible organ variously termed the crop (Clench & Kondo 1943) or esophagus (Speiseröhe of Bergh 1896; Ösophagus of Alpers 1931). Usually no digestion takes place in this organ, although enzymes may leak anteriorly from the intestine, causing some. Since there is no mechanism for trituration, prey in the esophagus is usually in a good state of preservation and identification is thus facilitated. The junction of the esophagus and intestine is marked by the entrance of two large ducts from the digestive glands. The prey is gradually moved from the crop into the intestine, where digestion and absorption occur. Fecal matter is not usually compacted into pellets but is excreted as undigested remains.

The piscivorous species represent an exception to the course of digestion just described, as noted by Kohn (1956b). Considerable digestion occurs in the anterior portion of the alimentary tract. The food swallowed is proportionately much larger than that

eaten by the other species, and the lower parts of the tract are not very distensible.

TIME OF FEEDING

Feeding takes place at night and usually not during daylight hours. This was demonstrated in the following manner. In analyses of alimentary tract contents, the position of food in the tract was recorded. Since the time of collection was noted, the position of food in the tract could be plotted against time of day. Food frequency histograms for the three dominant species on marine benches are shown for pertinent times of day in Fig. 24. Data from all marine bench stations are included. Data for three species on reef platforms are presented in Fig. 25. At other times of day (during afternoon and early evening) the proportion of snails with empty alimentary tracts was so high that it was not profitable to collect and examine large numbers of them.

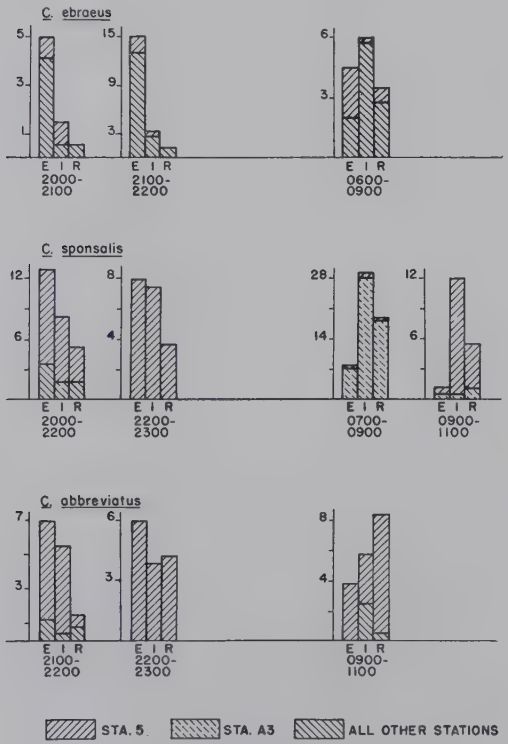


FIG. 24. Food in alimentary tracts of *Conus* collected at marine bench stations at different times of day. E = esophagus. I = intestine. R = rectum.

In Figs. 24 and 25, alimentary tracts are divided into esophagus (E), intestine (I), and rectum (R). The esophagus and intestine are quite distinct organs (Bergh 1896, Alpers 1931), while the rectum is somewhat arbitrarily considered as the region between the last curve of the intestine and the anus. The dat from marine benches show that, in all three species,

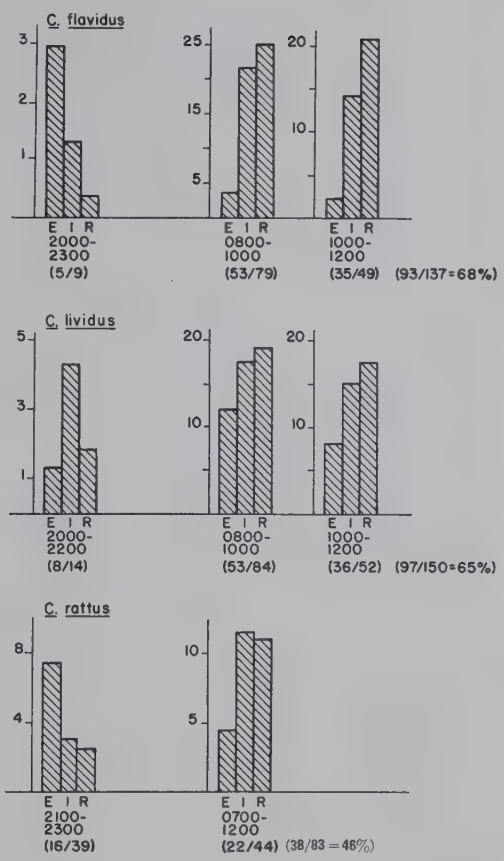


FIG. 25. Food in alimentary tracts of *Conus lividus*, *C. flavidus*, and *C. rattus* at different times of day. E = esophagus. I = intestine. R = rectum.

the crops contain the largest number of food organisms at night. By mid-morning, food has largely passed from the esophagus into the intestine and rectum, and incidence of esophagus contents is greatly reduced.

Of the dominant reef platform species, evidence of time of feeding was obtained for *Conus flavidus, C. lividus,* and *C. rattus,* as shown in Fig. 25. Nocturnal records for *C. flavidus* and *C. lividus* are probably too few to be meaningful. That feeding takes place at night in *C. flavidus* is plainly shown, however, by the low incidence of prey in the esophagus during the day. In *C. lividus,* the data are less clear-cut. This may be due to a slower rate of digestion, or some feeding may take place during daylight hours. *C. rattus* is plainly a nocturnal feeder. At night, prey organisms are found chiefly in the esophagus, while during the morning their remains occupy the lower regions of the alimentary tract.

The number of specimens examined which had food in the alimentary tracts is also indicated in Fig. 25. About two-thirds of the population of both *Conus*

TABLE 8. Prey Organisms Consumed by Vermivorous Species of *Conus* at Marine Bench Stations

	sponsalis				*abbreviatus*		*ebraeus*			*chaldaeus*			*rattus*	*lividus*			*flavidus*		*miles*	*distans*
Station	5	11	A3	T	5	T	5	11	T	5	11	T	T	5	11	T	5	T	T	T
No. Specimens Examined	45	51	92	258	158	243	94	5	122	25	12	59	79	10	1	24	6	10	1	2
Nereis jacksoni Kinberg var.	—	6	5	30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Perinereis helleri Grube	15	14	—	32	19	20	104	3	115	—	—	—	13	—	—	—	—	—	—	—
Platynereis dumerilii (Audouin & Edwards)	2	2	6	10	2	3	—	—	—	17	16	45	—	—	1	1	—	—	—	—
Nereid sp. 350	1	2	1	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Nereidae	—	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Nereidae	18	24	13	77	22	24	104	3	115	17	16	45	13	—	1	1	—	—	—	—
Lysidice collaris Grube	2	3	3	11	5	27	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Palola siciliensis (Grube)	—	—	—	—	—	—	3	3	7	4	—	8	—	—	—	—	—	—	—	—
Eunice antennata Savigny	—	1	1	2	1	2	—	—	—	—	—	—	12	—	—	—	—	—	—	—
Eunice (Nicidion) caribboea (Grube)	—	5	30	36	8	10	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Eunice filamentosa Grube	1	—	—	1	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Marphysa sanguinea (Montagu)	—	—	1	1	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eunice afra Peters	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Unidentified Eunicidae	1	—	—	1	1	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Lumbrinereis sarsi (Kinberg)	2	3	8	14	10	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arabella iricolor (Montagu)	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Eunicea	6	12	43	66	28	61	3	3	8	4	—	8	13	—	—	—	—	—	1	1
Nicolea gracilibranchus (Grube)	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	—	2	—	—
Terebellid sp. 837	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—
Cirriformia semicincta (Ehlers)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Polydorid sp. 1500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Unidentified annelids	—	1	3	6	4	4	1	—	1	—	—	—	—	—	—	2	—	1	—	—
Total Annelids	24	36	59	149	45	89	108	6	124	21	16	53	26	1	1	8	—	7	1	1
Total Identified Food	24	36	59	149	54	89	108	6	124	21	16	53	26	3*	1	16†	—	7	1	1
Unidentified Food	1	1	1	4	1	3	—	—	—	—	—	—	—	—	—	3	—	1	—	—

Data from Stations 5, 11, and A3 are entered separately as noted. T = Data from all bench stations.
Numbers in body of table indicate numbers of polychaete species at left found in alimentary tracts of *Conus* species at top.
Chief references used in the identification of the polychaetes were Abbott (1946), Hartman (1940, 1944, 1948), Holly (1935), Fauvel (1927), Okuda (1937), and Treadwell (1906, 1922).
*Includes one specimen definitely identified, and one tentatively identified, as *Ptychodera flava laysanica* Spengel.
†Includes five specimens definitely identified, and three tentatively identified, as *Ptychodera flava laysanica* Spengel.

flavidus and *C. lividus*, and about one-half of the population of *C. rattus* succeed in capturing food each night.

Investigation of the rate of passage of food through the alimentary tract of *Conus abbreviatus* showed that the food starts passing into the intestine after about 1.5 hrs in the esophagus. After about 3 hrs, fecal matter is present in the rectum. From 12-24 hrs after feeding, the alimentary tract is completely emptied. Therefore, gastropods observed with empty tracts in the afternoon may or may not have fed the previous night.

NATURE OF THE FOOD OF *Conus* ON MARINE BENCHES

Solution Bench Stations. Of the eight species of *Conus* present at Station 5, five, including the four dominant species, were found to feed exclusively on polychaete annelids. Of the less abundant species, *C. flavidus* feeds predominantly on polychaetes but may occasionally take an unsegmented worm. *C. lividus* feeds on the enteropneust *Ptychodera flava* but consumes polychaetes as well. *Ptychodera* is a sand-dwelling worm and is uncommon on marine benches. Both *C. flavidus* and *C. lividus* prefer Terebellidae among the polychaetes. These worms are also typically sand dwellers, building tubes on the sides of rocks partly buried in sand. The low abundance of *Ptychodera* and terebellids on benches may limit the populations of *C. lividus* and *C. flavidus* in this habitat.

Conus pennaceus was earlier reported (Kohn 1955) to feed on other gastropods. Small species of the type on which *C. pennaceus* thrives (especially *Haminoea*) are abundant on benches, so the low

density of *C. pennaceus* does not seem the result of limited food supply. Rather, *C. pennaceus* is probably limited by lack of sufficient sand in which to burrow during the day.

Contents of alimentary tracts of 343 specimens collected at Station 5 were determined by dissection of fixed specimens or collection of fecal matter from living individuals. From these, 210 prey organisms were identified, 199 of them to species. All eight species of *Conus* are represented in the sample, but food remains were not found in any alimentary tracts of the few *C. rattus* and *C. pennaceus* examined. The results are summarized in Table 8, which also includes totals from other bench stations for comparison.

These data show that at Station 5, *Perinereis helleri* is the primary food of the three most abundant species of *Conus*. *C. ebraeus* eats this species almost exclusively, while *C. abbreviatus* especially feeds on other polychaetes as well. Members of the superfamily Eunicea (only the families Eunicidae, Lumbrinereidae, and Arabellidae are represented) are eaten about as often as nereids. *C. sponsalis*, on the other hand, is more restricted to nereids. This may reduce the possibility of competition for food between these two species, which feed in the same zone of the bench. Most of the population of *C. ebraeus* is found feeding in the central portion of the bench (Fig. 20) and is thus seeking *P. helleri* in a different place from *C. sponsalis* and *C. abbreviatus*.

The food of the fourth commonest species, *Conus chaldaeus*, is strikingly different. *C. chaldaeus* also feeds exclusively on a single species of nereid, but its food is *Platynereis dumerilii*, which occurs predominantly toward the outer edge. A large substratum sample collected near the outer edge at Station 5, adjacent to two specimens of *C. chaldaeus*, contained the following Nereidae:

Platynereis dumerilii	16
Nereis jacksoni	14
Perinereis helleri	1
Unidentified epitokes	3

Thus *P. dumerilii* is an order of magnitude more abundant than *P. helleri* near the outer edge. The prey species of *C. chaldaeus* is thus correlated with the distribution pattern across the reef platform, as both prey and predator are less abundant near shore.

The three most abundant species of *Conus* exert an active demand on the local population of *Perinereis helleri*. If this demand were found to exceed the immediate supply of the prey species, it could be said that the three predator species compete with each other for this food, at least in areas of distribution overlap.

Food organisms were found in about 60% of all alimentary tracts of specimens examined from Station 5. Since specimens were collected at all hours, and since feeding has been shown to take place only at night, it is possible that some individuals had defecated remains of the previous night's meal before being examined. A mean of one polychaete per gastropod per night is a reasonable estimate of feeding rate.

The mean density of the *Conus* species that feed on *Perinereis helleri* is 2/100 sq ft. Since *P. helleri* constitutes about 74% of their diet, these species consume an average of 1.5 individuals of *P. helleri*/100 sq ft/night, or 0.17/m.^{2}/night. Substratum samples taken about halfway across the bench contained the densities of nereids shown in Table 9. At the calculated feeding rate, about 28 years would be required to exhaust the observed population of *P. helleri*, considering no replacement.

TABLE 9. Population Density of Nereidae and Eunicea Halfway Across Station 5.

Species	No. counted in 625 cm.^{2}	No./m.^{2}	Eaten by *Conus* /m.^{2}/day
Perinereis helleri....	121	1,940	0.17
Nereis jacksoni.....	267	4,270	
Platynereis dumerilii.	7	112	
All Eunicea.....	4/30 cm.^{2}	1,300	

Although the smaller *Nereis jacksoni* was more abundant than *Perinereis helleri* at Station 5, it was not found to be eaten by *Conus*. Elsewhere it is eaten by *C. sponsalis* (Table 8).

The feeding habits of the species at Station 11 are shown in Table 8 to be essentially similar to those at Station 5. In addition, the few specimens of *Conus rattus* collected there were found to consume both nereid and eunicid polychaetes. The single specimen of *C. catus* collected had an empty alimentary tract.

No quantitative samples of polychaetes at Station 11 were analyzed. However, *Perinereis helleri* was observed to be common. Each of two samples, representing a few square centimeters of substratum surface, contained 9 polychaetes, of which 3 and 5, respectively, were *P. helleri*. Standing crop is probably of the same order as at Station 5.

Water-leveled Bench Stations. Alimentary tracts of 92 specimens of *Conus sponsalis* from Station A3 were analyzed. Of these, 90 were collected between the hours 0700 and 0900. Polychaete remains were found in 55 specimens. The frequency distribution of remains in alimentary tracts is shown in Fig. 24. The low frequency of esophagus contents indicates that feeding had ceased some time before collection, probably at or before dawn. Most of the remains are seen to be in the intestine and/or rectum. This is in essential agreement with data from other stations.

Fifty-two of the specimens examined contained remains of one polychaete in each, two contained remains of two polychaetes each, and one contained remains of three polychaetes. It may be concluded that most individuals succeed in capturing one polychaete per night.

The nature of the food of *Conus sponsalis* at Station A3, shown in Table 8, differs markedly from that

of other bench stations. The primary prey organism is not a nereid, but the eunicid, *Eunice (Nicidion) cariboea*. *Perinereis helleri* was not found to be eaten at all (but its presence at Station A3 was not ascertained). This resulted in eunicids far exceeding nereids in the prey of *C. sponsalis* at Station A3, in contrast with other stations studied. This may be correlated with the fact that *C. abbreviatus*, which generally (Table 8) feeds on eunicids more often than nereids, is virtually absent from Station A3. It may be conjectured that where the two co-occur, they compete for eunicids, with the result that *C. abbreviatus* is the more successful, and *C. sponsalis* is forced to eat nereids, which are possibly less desirable as food. When *C. abbreviatus* is excluded for other reasons from a microhabitat where *C. sponsalis* does occur, the latter species would then be able to exploit eunicids as food.

As for other polychaete feeders at Station A3, remains of *Eunice antennata* were found in three of the seven specimens of *Conus rattus* which were examined, and the single *C. abbreviatus* had fed on a *Lysidice collaris*.

The food of *Conus catus* has previously been shown to be small fishes, chiefly blennies and gobies, and the feeding process has been briefly described (Kohn 1956b). Remains of fishes were found in two of the three specimens collected at Station A3. One of the fishes was identified as the goby, *Bathygobius fuscus*. The other was too poorly preserved to permit identification. The food of *C. catus* at bench stations is summarized in Table 10.

TABLE 10. Prey Organisms Consumed by *Conus catus* at Marine Bench Stations.

	Sta. K1	All Bench Stations
No. Specimens Examined	13	24
Bathygobius fuscus (Rüppell)	2	3
Istiblennius gibbifrons (Quoy and Gaimard)	3	3
Unidentified fishes	2	5
Total Fishes	7	11
Unidentified fecal matter		1

Only small samples of most species from Station K1 were examined for alimentary tract contents. The expected prey organism, *Perinereis helleri*, dominated in *Conus sponsalis* and *C. ebraeus*. Nine of 10 food organisms isolated from *C. abbreviatus* were *Lysidice collaris*. Thirty-eight specimens of *C. rattus* were analyzed. Eleven contained remains of *P. helleri*, one, *Eunice antennata*, and the remaining 26 were devoid of identifiable food. Results of analysis of alimentary tracts of 13 specimens of *C. catus* are shown in Table 10. The single specimen of *C. retifer* was found to have an empty alimentary tract. However, other members of its subgenus (*Cylinder*) feed exclusively on other gastropods, and it is likely that *C. retifer* does also.

Polychaetes did not appear as abundant as on solution benches, but no quantitative samples were collected. *Perinereis helleri* and *Lumbrinereis* sp. 239 were observed to be present. Three of the eight species of *Conus* collected feed primarily on *P. helleri*. It is not known whether the demand exceeds the immediate supply and, therefore, whether food is the requisite which governs population size. The possibility of competition for food between *C. catus* and the other species present is entirely precluded, as it feeds on fishes.

FOOD PREFERENCE

Of the species of *Conus* characteristic of the marine bench habitat, *C. sponsalis* and *C. abbreviatus* have been shown to be most similar to each other with respect to feeding habits and pattern of distribution. Both species feed exclusively on polychaetes. Frequency of different prey species found in alimentary tracts is shown in Table 8. If data from all marine benches studied are combined (Column T), polychaetes of the superfamily Eunicea comprise 68%, and Nereidae 26% of the diet of *C. abbreviatus*. The diet of *C. sponsalis* consists of 44% Eunicea and 52% Nereidae. Although feeding habits are rather similar, the difference between the two species is significant ($P = 10^{-3}$) in the samples analyzed.

Polychaetes of both groups are abundant (Table 9). The observed differences in feeding frequency may be accounted for by two alternative hypotheses: (1) *C. abbreviatus* is better adapted to feeding on eunicids, which burrow into limestone and coral, than on nereids, which occur epifaunally among the holdfasts of algae. Conversely, *C. sponsalis* is better adapted to feeding on nereids than eunicids. (2) *C. abbreviatus* exhibits active preference for eunicids over nereids, and *C. sponsalis* prefers nereids to eunicids.

Comparison of results of food studies at Station A3 with other stations provided at least some evidence in favor of the view that, where the two species co-occur, *C. abbreviatus* is the more efficient predator on eunicids.

The second hyopthesis was tested experimentally in a choice chamber, following the method of Van Dongen (1956). The chamber was a lead-sheathed wooden sea water table 125 × 58 cm in area and 8 cm deep (Fig. 26). Polychaetes were placed in Bull Durham bags, which were secured to the chamber floor. The water current thus passed over the polychaetes and then over the snails. All stimuli received by *Conus* from the polychaetes were thus of a chemical nature. Actual predation was prevented by the cloth bags, from which snails were unable to extract the polychaetes. In each experiment, one or two polychaetes were placed in each bag, and 12-59 specimens of a single species of *Conus* were placed at a distance of 88 cm from the goal (Line cd, Fig. 26).

Experiments were usually begun in late afternoon and allowed to continue overnight, to coincide with the snails' normal food-seeking regimen. A few of

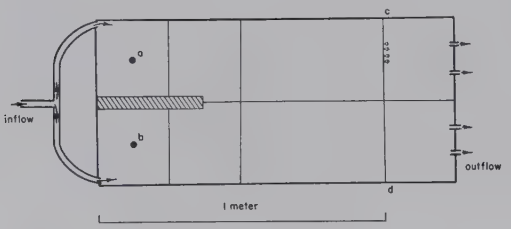


FIG. 26. Choice chamber for determination of food preferences of *Conus*. Lines were marked on floor of chamber as shown. During an experiment, fresh sea water was admitted to the chamber equally through the two inflow tubes. Outlets were located 1 cm above the chamber floor, so that a uniform depth of 1 cm of water was maintained in the chamber. A wooden partition (hatched) 40 cm in length partially separated the two portions of the chamber. This served to prevent mixing of stimuli and alteration of choice by snails. Food chambers are shown at a and b. Line cd is the starting line along which snails were placed at outset of an experiment.

the experiments with *Conus sponsalis* were allowed to run 40 hrs. At the termination of an experiment, snails were scored as having reached to within 25-50 cm of the goal, less than 25 cm, or adjacent to the food chamber. In the summary of results (Table 11), all three categories are summed.

TABLE 11. Summary of Results of Food Choice Experiments with *Conus sponsalis* and *C. abbreviatus*.

Number of Experiments	Number of Snails	Nereidae* Chosen	Eunicidae Chosen
C. sponsalis			
6	222	42	28**
2	61	22	2***
Total 8	283	64	30
C. abbreviatus			
2	87	17	35**

Figures in body of table indicate number of snails choosing polychaete listed above in choice chamber experiments.
*=*Perinereis helleri*
**=*Eunice antennata*
***=*Palola siciliensis*

Table 11 shows that, given equal choice of both, *Conus abbreviatus* chooses the eunicid (*Eunice antennata*) more often than it chooses the nereid (*Perinereis helleri*). *C. sponsalis* chooses the nereid (*P helleri*) more often than either of the eunicids tested (*E. antennata, Palola siciliensis*). The difference in preference for eunicids and nereids between *C. sponsalis* and *C. abbreviatus* is highly significant ($P < .01$).

Comparison of Food in Nature and Choice Experiments. A comparison between the experimental choices and food in nature is made in Table 12. Since the percentages given do not permit direct comparison between the experiments and nature, the ratios of eunicids to nereids for *Conus abbreviatus* and *C. sponsalis* are included. Variation of the relative frequency of predation on nereids and eunicids in nature from the frequency of choice in the experiments is significant for *C. sponsalis* ($P = .05$) but not for *C. abbreviatus* ($P \gg .1$).

TABLE 12. Comparison of Results of Choice Chamber Experiments with Food Habits of *Conus sponsalis* and *C. abbreviatus* in Nature.

	Food in Nature (all marine benches)	Choice in Experiments
C. sponsalis		
Nereidae	52%	23%
Eunicea	44%	11%
Ratio E:N	1:1.3	1:2.1
C. abbreviatus		
Nereidae	26%	20%
Eunicea	68%	40%
Ratio E:N	2.6:1	2.0:1

Comparison of data for nature and experiments shows that the food of *Conus sponsalis* and *C. abbreviatus* in nature is reflected in the choice experiments. The partition of the environment into different but overlapping microhabitats which occurs with respect to food may therefore be maintained by active preference of different prey species by the two predator species.

The hypothesis that *Conus sponsalis* is better adapted to feeding on nereids than eunicids was not amenable to experimental test. It has been suggested, however, that information bearing on this question might be gained from study of radula morphology (Peile 1939).

Although the anterior extremities of radula teeth show considerable variation throughout the genus *Conus*, the teeth may be grouped in two categories with respect to the posterior portion, or base. In the first, the base is simple and of more or less greater diameter than the shaft, thus forming a terminal knob. The base in the second group is characterized by the presence of a forward projecting cone (Fig. 27).

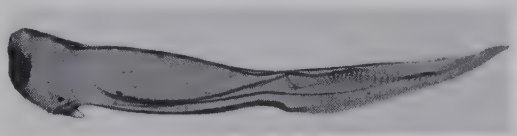


FIG. 27. Radula tooth of *Conus abbreviatus*. The forward projecting cone is visible at the left.

Peile (1939) made the plausible suggestion that this cone might serve to retain the tooth within the proboscis when prey is attacked. It was shown, however, that *C. striatus* which does not possess such a cone, retains the tooth in the proboscis in feeding (Kohn 1956b).

It will be shown below that the presence of the forward projecting cone is generally correlated with feeding on eunicid and other tube-dwelling polychaetes in nature. Eunicids, unlike nereids, live in burrows in coral and reef rock, and the basal cone may well aid the predator in extracting the worm from its burrow.

TABLE 13. Prey Organisms Consumed by Vermivorous Species of *Conus* at Subtidal Reef Stations. Numbers in body of table indicate number of polychaete species at side found in alimentary tracts of *Conus* species at top.

	sponsalis			*abbreviatus*				*ebraeus*				*chaldaeus*		*miles*		*rattus*			*distans*	
Station	7	R	T	3	9	R	T	3	9	R	T	R	T	R	T	15	R	T	R	T
No. specimens examined	64	72	330	19	24	99	342	15	8	55	199	4	106	11	20	18	55	149	19	21
Nereis jacksoni Kinberg var.	4	4	34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Perinereis helleri Grube	3	3	35	—	—	—	20	—	1	6	136	—	5	—	—	7	7	21	—	—
Platynereis dumerilii A. & E.	3	3	13	—	—	—	3	—	—	—	—	2	98	—	—	—	1	1	—	—
Nereid sp. 350	1	1	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Nereidae	1	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Nereidae	12	12	89	—	—	—	24	—	1	6	136	2	103	—	—	7	8	22	—	—
Lysidice collaris Grube	6	6	17	—	—	9	36	—	—	2	2	—	—	5	16	—	—	—	—	—
Palola siciliensis (Grube)	—	—	—	1	—	1	1	14	8	29	44	—	14	—	—	—	—	—	—	—
Eunice antennata Savigny	1	1	3	5	10	20	22	—	—	—	—	—	—	1	1	3	17	29	1	1
Eunice (*N.*) *cariboea* Grube	—	3	39	—	—	4	14	—	—	1	1	—	—	—	—	1	1	2	—	—
Eunice afra Peters	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	9	9	12	13
Marphysa sanguinea Montagu	—	—	1	1	1	3	6	—	—	—	—	—	—	—	—	—	—	—	—	—
Eunice filamentosa Grube	—	—	1	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Eunicidae	—	—	1	1	—	1	2	—	—	—	1	—	1	—	—	—	—	—	—	—
Lumbrinereis sarsi (Kinberg)	2	3	17	—	—	—	11	—	—	—	—	—	—	—	—	—	—	—	—	—
Arabella iricolor (Montagu)	—	—	—	—	—	5	9	—	—	—	—	—	—	—	—	—	—	—	—	—
Total Eunicea	9	13	79	8	11	43	104	14	8	32	48	—	15	6	17	8	27	40	13	14
Eurythoe complanata (Pallas)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Annelids	1	1	7	—	—	—	4	—	—	1	2	—	—	—	—	—	—	—	—	—
Total Annelids	22	26	175	8	11	43	132	14	9	39	186	2	118	6	17	15	35	62	13	14
Total Identified Food	22	26	175	8	11	43	132	14	9	39	186	2	118	6	17	15	35	62	13	14
Unidentified Food	2	2	6	—	—	—	4	—	—	—	—	—	1	—	—	—	—	—	1	1

SUMMARY OF FOOD OF *Conus* IN THE MARINE BENCH HABITAT

Conus abbreviatus and *C. sponsalis,* both of which possess the small cone at the base of the radula tooth, feed on polychaetes which belong to different groups, the Nereidae and Eunicea, and differ ecologically as noted above. Although there is overlap (63%), the difference in numbers of the two groups of prey organisms eaten by *C. abbreviatus* and *C. sponsalis* is highly significant ($P = 10^{-3}$). Comparison by individual species of the food eaten by these two *Conus* species on all bench stations (Table 8) revealed overlap of only 25% and the probability of only 10^{-6} that the polychaetes preyed on represented random samples from the same population. Differences between the species composition of the food of *C. sponsalis* and *C. abbreviatus* are thus sufficiently great that competition for food is unlikely.

Of the other species which occur in the marine bench habitat, *Conus ebraeus* and *C. chaldaeus* do not possess the forward projecting cone on the radula tooth. Both species are extremely oligophagous. Nereids comprise 85% of the food of *C. chaldaeus* and 93% of the food of *C. ebraeus.* The two species do not differ significantly in the proportion of the diet comprised by nereids ($P = .24$). In striking contrast to this, however, is the specific nature of the prey eaten, as shown in Table 8. In the samples collected on all marine benches, the only nereid eaten by *C. ebraeus* was *Perinereis helleri,* while the only nereid eaten by *C. chaldaeus* was *Platynereis dumerilii.* Despite the fact that both predators are typically found on the same benches, and with overlapping distributions, they were never found to eat the "wrong" polychaete in the bench habitat.

Unfortunately, no choice experiments were carried out in order to test the possibility of differences in active preference of prey species by *Conus ebraeus* and *C. chaldaeus.* It is likely that the specific differences in prey are correlated with differences in the ecology of the prey species. In Table 9 *Perinereis helleri* was shown to be two orders of magnitude more abundant than *Platynereis dumerilii* about halfway across the bench at Station 5, where *C. ebraeus* is maximally abundant. Nearer the outer edge, where *C. chaldaeus* reaches its peak density, *P. dumerilii* is an order of magnitude more abundant than *P. helleri.*

R = All reefs; T = All stations; * = All from Station 4; + = Equals Total.

vexillum			*vitulinus*	*imperialis*	*pulicarius*		*flavidus*				*lividus*					
9	R	T	T*	R+	9	R+	3	9	R	T	3	7	9	R	T	Station
13	16	17	4	31	11	20	47	56	182	192	32	46	34	216	240	No. Specimens Examined
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*Nereis jacksoni* Kinberg var.
—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	*Perinereis helleri* Grube
—	—	—	—	—	—	—	—	—	—	—	1	5	—	11	12	*Platynereis dumerilii* A. & E.
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Nereid sp. 350
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Unidentified Nereidae
—	—	—	—	—	—	—	—	—	—	—	1	5	—	11	12	Total Nereidae
—	—	—	—	—	2	2	5	5	24	24	—	—	—	—	—	Capitellid sp. 1040
—	—	—	—	—	—	—	—	—	11	11	—	—	—	—	—	*Thelepus setosus* Quatrefages
6	9	9	—	—	—	—	13	5	22	22	—	—	—	1	1	*Polycirrus* sp. 660
—	—	—	—	—	—	—	—	—	2	5	—	—	1	1	1	Terebellid sp. 837
—	—	—	1	—	—	—	10	17	32	34	2	—	—	7	11	*Nicolea gracilibranchus* (Grube)
5	6	6	—	4	—	—	—	—	—	—	—	—	—	1	2	Unidentified Terebellidae
—	—	—	—	—	—	—	23	22	67	72	2	—	1	10	15	Total Terebellidae
—	—	—	—	—	—	—	—	—	5	5	—	—	—	1	1	Polydorid sp. 1500
—	—	—	—	—	—	—	—	—	1	1	—	1	1	4	5	*Cirriformia semicincta* (Ehlers)
11	15	15	1	4	—	—	—	—	—	—	—	—	—	2	2	*Lygdamis nesiotes* (Chamberlin)
—	—	—	—	11	—	—	—	—	—	—	—	—	—	3	3	*Sabellastarte indica* Savigny
—	—	—	—	—	—	—	1	3	4	5	—	1	—	2	3	Unidentified Annelids
11	15	15	1	15	—	—	29	30	101	108	3	7	2	33	41	Total Annelids
					—	2	—	—	—	—	—	—	—	—	—	*Thalassema* sp.
					—	—	1	—	1	1	13	5	8	28	33	*Ptychodera flava laysanica* Spengel
					—	—	—	—	1	4	2	5	6	29	32	*P. flava laysanica* Spengel (tentative identification)
					—	—	—	—	—	—	—	—	1	1	1	*Octopus* sp.?
11	15	15	1	15	2	4	30	30	106	113	18	17	16	90	106	Total Identified Food
2	—	2	1	2	—	3	7	5	18	21	5	10	6	39	42	Unidentified Food

Conus rattus, the other vermivorous species characteristic of marine benches, does possess the basal cone on the radula tooth. It feeds predominantly on eunicids (Table 8) and in the proportion of Eunicea eaten does not differ significantly from *C. abbreviatus*. However, the specific nature of the food of these two species is significantly different ($P = 10^{-6}$). In fact, the nature of the food of each vermivorous species of the marine bench habitat differs significantly from that of all others at the 1% level. Thus these species, as well as *C. catus* which eats only fishes, avoid interspecific competition for food in the bench habitat.

Nature of the Food of Conus on Subtidal Reefs

Of the 16 species of *Conus* collected by the writer on reef platforms, 10 were found to feed exclusively on polychaetes. These are *C. abbreviatus, C. ebraeus, C. sponsalis, C. rattus, C. imperialis, C. chaldaeus, C. vexillum, C. distans, C. vitulinus,* and *C. miles.* Polychaetes constitute more than 90% of the food of *C. flavidus,* which occasionally consumes an unsegmented worm. Polychaetes comprise about 50% of the food of *C. lividus,* which feeds also on an enteropneust. *C. pulicarius* feeds on polychaetes and echiuroids, as far as is known. *C. pennaceus* and *C. marmoreus* feed on other gastropods, and *C. striatus* feeds on fishes.

VERMIVOROUS SPECIES

Species Typical of Marine Benches Which Occur also on Reef Platforms. The species composition of the food of the vermivorous species of *Conus* which occur on reef platforms is given in Table 13 for a sample of 784 specimens of 13 species. From these, 360 prey organisms were identified, 254 of them to species. Most of the records are determinations of alimentary tract contents of fixed specimens. A few represent collection of fecal matter from living individuals. Total data for certain species include records from marine bench and deep water habitats for comparison.

The more diversified food on reefs in comparison with marine benches is made possible by the addition of the sand substratum microhabitat on reef platforms. All of the prey species listed in Table 13 but not in Table 8 are associated with the sand substratum. All but one of the polychaetes eaten by

Conus on marine benches were found to be present and eaten on reef platforms. The limestone outcrops and coral of the reefs provide abundant burrowing sites for eunicids. Nereids, however, are not common on the reefs, except where an algal turf is present on exposed limestone. This is especially reflected in the feeding habits of *C. sponsalis, C. abbreviatus, C. ebraeus,* and *C. rattus. Perinereis helleri* is the dominant prey of each of these species on marine benches (Table 8), but it is much less important to all four on reefs, where it is less abundant.

On reef platforms, *Conus sponsalis* is often found in regions of dead coral and reef limestone which support an algal turf and nereids, as well as eunicids. Both groups of polychaetes are eaten by *C. sponsalis,* in frequencies which do not differ significantly from those eaten by marine bench populations of this species.

No nereids were found in alimentary tracts of 99 specimens of *Conus abbreviatus* collected on coral reefs. This is as expected, since on reef platforms *C. abbreviatus* is not found on the algae-matted areas where some nereids occur. Eunicea, which commonly burrow into any available limestone on coral reefs (Hartman 1954), apparently constitute the entire diet of *C. abbreviatus.* The frequency of different polychaete species eaten differs significantly between bench and reef populations of *C. abbreviatus.* This is due largely to the predominance of *Eunice antennata* as prey in the latter habitat.

The food of *Conus ebraeus* in reef habitats also varies from that on marine benches in the direction of increased concentration on a species of eunicid. In contrast with the previous species, however, *C. ebraeus* feeds chiefly on *Palola siciliensis* and does not eat *Eunice antennata.*

The most obvious difference between the ecological niches of *Eunice antennata* and *Palola siciliensis* is that the latter species is typically found in more dense limestone. This observation is correlated with the fact that the mandibles are larger and stronger in *Palola* than in the other genera of Eunicea. (This has been discussed by Hartman (1954), who suggests that *Palola* may be the most destructive of the Eunicea to coral reefs. Following the same criterion, *Lysidice, Eunice, Marphysa, Lumbrinereis,* and *Arabella* would follow in order of decreasing destructiveness.) Filamentous algae were observed in intestines of *E. antennata.* These are perhaps the boring forms recently discussed by Odum & Odum (1955). The food of *P. siciliensis* was not determined. Takahashi (1939) concluded that several eunicids inhabiting coral reefs are omnivorous, consuming sand, diatoms, crustaceans, and algal fragments.

Conus chaldaeus occurs rather rarely on reef platforms. *C. rattus,* on the other hand, is about as common as it is on marine benches. As in other species common to both habitats, eunicids are consumed significantly more often than nereids ($P = .03$) by reef than bench populations of *C. rattus.*

In summary, there is virtually no qualitative difference in the specific nature of the prey eaten by those species of *Conus* common to both the reef and bench habitats. The frequencies of the different species eaten vary considerably, however, and are correlated with differences in substratum characteristics of the two habitats.

Typical Reef Platform Species. The most abundant species of *Conus* on subtidal reef platforms were shown (Figs. 14-17, 19) to be *C. flavidus* and *C. lividus.* Prey organisms recovered from alimentary tracts of about 200 specimens of each of these species are listed in Table 13. It is readily apparent that *C. flavidus* feeds almost exclusively on polychaetes, that the largest single item in the food of *C. lividus* is the enteropneust, *Ptychodera flava,* and that these species feed only occasionally or never on nereids and eunicids.

Tubicolous polychaetes comprise almost the entire diet of *Conus flavidus.* About two-thirds of these are members of the family Terebellidae. The other main prey species is an unidentified species of the family Capitellidae. The terebellids on which *C. flavidus* feeds live in tubes which are usually attached to the under sides of coral rocks or pieces of rubble resting in sand. The intestines of these polychaetes are usually filled with extremely fine sand particles. The terebellids are probably selective deposit feeders, selection apparently being effected by the tentacles.

Conus flavidus consumes enteropneusts only occasionally. In contrast, *Ptychodera flava* constitutes about 50% of the diet of *C. lividus.* Since it has no hard parts, *P. flava* is particularly difficult to identify in the partially digested state. The reddish eggs, which are apparently refractory to the digestive enzymes of *Conus,* aided identification of the females eaten. However, a number of *C. lividus* alimentary tract contents, which appeared to be remains of *Ptychodera,* could not be positively identified. These are entered separately in Table 13, but they are included in "total identified food."

The ecological niche of *Ptychodera flava* differs markedly from those of the terebellids on which *Conus lividus* feeds less often. Although all are deposit feeders in the same habitat, *P. flava* moves slowly about through the sand. It appears to be a nonselective feeder, ingesting in the manner of an earthworm. A wide range of sand particle sizes is found in its alimentary tract. As there is no apparent mechanism for trituration, the particle size distribution in the tract is presumably identical with that of the environment, but this was not determined.

The feeding of *Conus lividus* on *Ptychodera flava* was observed in the laboratory. When both were placed in a dish of sea water, the rostrum, but not the proboscis, of *Conus* was extended. When the mouth touched the worm, the latter was engulfed without being stung. During the entire engulfment process, which lasted only about 15 sec, the *Ptychodera* continued its normal peristaltic pulsations. This method of feeding may not be duplicated in nature. The observed presence of radula teeth in the ali-

mentary tract with food remains indicates that *C. lividus* stings *Ptychodera* as well as polychaetes before feeding.

Other Reef Species. The remaining six reef-inhabiting vermivorous species together comprise only about 6% of the total population of *Conus* in this habitat. It was possible to collect and analyze only small samples, but the results obtained are of considerable interest and are included in Table 13 for completeness.

The most common of these species is *Conus imperialis.* Only two prey species were found in analyses of alimentary tract contents and recovery of fecal matter of 31 specimens. One of these was the eunicid, *Marphysa sanguinea,* which is also eaten to some extent by other species of *Conus.* Notes on the ecology of this polychaete were recorded by Abbott (1946), who stated that "this species has been found only in limited areas of the pond [Wailupe Fish Pond, Oahu] where the bottom is sandy and the salinity close to that of sea water. Here it occurs under rocks, and does not appear to burrow deeply into the sand. It has not been found in regions where a soft mud bottom prevails."

The more common prey of *Conus imperialis* is the amphinomid polychaete *Eurythoe complanata.* Although this species is the most conspicuous polychaete on Hawaiian coral reefs, it was never found to be eaten by any other species of *Conus. Eurythoe* possesses extremely abundant large setae, which easily penetrate human skin and cause a burning sensation. They may possess a venom (Halstead 1956). Nevertheless, intestines of *C. imperialis* were often observed literally packed with these setae. The polychaete is typically found under rocks or in crevices in coral. Its food is unknown.

On several occasions, specimens of *Eurythoe complanata* were fed to *Conus imperialis* in the laboratory. The stinging operation is typical. Like *C. striatus, C. imperialis* uses its radula tooth as a harpoon. The tooth is not freed from the proboscis, but the impaled prey is drawn into the mouth by rapid contraction of the proboscis.

Only four prey organisms were recovered from the alimentary tracts of 20 specimens of *Conus pulicarius* which were examined. These were sufficient to show that the food of this species is not restricted to polychaetes. Two of the food organisms were of the species of capitellid eaten by *C. flavidus,* but the other two were of the echiuroid worm, *Thalassema* sp. Both of the latter were regurgitated by the snails after capture. At least one of the echiuroids was alive when regurgitated. This suggests that *Thalassema* may not be stung before being swallowed by *C. pulicarius.*

All of the other four vermivorous species of *Conus* collected on the reefs may be restricted to Eunicidae for food, although the samples examined were small. The primary food of *C. distans* is *Eunice afra.* This polychaete was found most commonly completely buried in coral rocks or in coral or other calcareous encrustation on basalt boulders. *C. miles* feeds chiefly on *Lysidice collaris,* and *C. vexillum,* on *Eunice antennata* and *Marphysa sanguinea.* A single specimen of *E. afra* was recovered from the alimentary tract of *C. vitulinus.*

The large differences in the specific nature of the prey of the vermivorous species of *Conus* on reef platforms would seem to virtually preclude the possibility of interspecific competition for food. It was nevertheless of interest to obtain some information on the abundance of the prey species.

In order to determine the species and abundance of polychaetes associated with, or burrowing into, limestone, coral and coral ruble, sample blocks of substratum were removed from reefs and placed in sea water in sealed jars. When the oxygen tension decreased, the polychaetes were attracted out of their burrows and eventually fell to the bottom of the jar. After 2-3 days, the contents of the jar were fixed in 10% formalin. Cracking of pieces of coral revealed few or no polychaetes remaining within the blocks after this treatment. Dry weight, volume and surface (projection) area of the blocks were determined. Polychaetes equal to or greater than 0.3 mm in maximum diameter were identified and preserved.

The results of samples from Stations 3 and 7 treated in this manner are shown in Table 14. In suitable areas on reefs eunicids are seen to be extremely abundant. It is difficult, however, to assess the density of polychaetes over the entire reef platform, since the relative areas of different types of substratum could not be adequately measured. The data in Table 14 probably give the correct order of magnitude for areas with a predominantly lithified substratum.

MOLLUSCIVOROUS SPECIES

Two species of *Conus* found on subtidal reef platforms appear to feed exclusively on other gastropod mollusks. The species composition of their prey, as well as that of *C. textile,* found rarely on reefs, is shown in Table 15. In addition to specimens collected on reefs, total data include material collected in deeper water.

At least 13 species of prosobranchiate and opisthobranchiate gastropods were recorded from alimentary tract analyses of 146 specimens of *Conus pennaceus.* The most common food species is the bubble shell, *Haminoea crocata.* Second commonest is the small prosobranch, *Phasianella variabilis.* Since the shells of prosobranchs are not swallowed, the identification of partly digested remains was extremely difficult. About half of the prey organisms were identified to species, but this was not possible in some which were represented only by radulae and/or opercula.

Feeding of *Conus pennaceus* on *Haminoea crocata, Terebra gouldii* Deshayes, and *Cypraea maculifera* (Schilder) was observed in the laboratory. A specimen of *Cypraea moneta* Linné was not eaten, however, when left in a tank with two *C. pennaceus* for 24 hr. *C. pennaceus* did not prey on other species of *Conus,*

TABLE 14. Abundance of Polychaetes Associated with Hard Substrata on Reefs.

Sample No.	Station	Area (cm.²)	Species	Number Present
1269	7	50	*Eunice (Nicidion) cariboea*	6
			Cirriformia semicincta	2
			Eunice antennata	1
			Unidentified Polychaetes	6
				—
			Total	15
			Density of Large Polychaetes	3,000/m.²
			Density of Eunicidae	1,800/m.²
			(Number of Polychaetes <0.3 mm. diameter in sample	51)
1276	3	129	*Eunice antennata*	5
			Palola siciliensis	4
			Lysidice collaris	3
			Eunice (Nicidion) cariboea	2
			Cirriformia semicincta	1
			Eurythoe complanata	1
			Platynereis dumerilii	1
				—
			Total	17
			Density of Large Polychaetes	1,300/m.²
			Density of Eunicidae	1,100/m.²

although several were retained in the same aquaria for several months.

The most striking aspect of the food of *Conus marmoreus* is that it appears to consist entirely of other species of *Conus*. Remains of *Conus* species were found in alimentary tracts of five of the seven specimens of this rather rare species which were examined. On 31 March 1956, Mr. Charles Sueishi observed a specimen in the act of feeding on *Conus abbreviatus* near Station 11. Dissection revealed the remains of a second *C. abbreviatus* in the intestine. On 6 July 1956, the writer observed a specimen in the act of feeding on *C. lividus* at Station 9.

A specimen of *Conus textile* collected at Station 15 by Miss Valerie Lang contained the radula sheath, operculum, and other remains of a *Conus pennaceus* in its alimentary tract. Another specimen, which had just eaten a *Conus striatus*, was collected by Dr. C. M. Burgess near Makua, Oahu. One other gastropod, a *Morula ochrostoma* (Blainville), was identified from the alimentary tracts of *C. textile* examined. In the laboratory, specimens of *C. textile* were observed to sting and consume *C. abbreviatus, C. ebraeus, C. lividus, Cypraea caputserpentis, Cypraea moneta, Turbo intercostalis* Menke, Thais *aperta* Blainville, and *Drupa morum* Lamarck, but they did not sting *C. flavidus* or *Helcioniscus argentatus* Nuttall.

PISCIVOROUS SPECIES

Conus striatus occurs sparsely on Hawaiian reef platforms. Remains of fishes from the five specimens which were examined could not be identified. A goatfish (*Parupeneus* sp.) is known to be eaten by *C. striatus* in Micronesia (unpublished data). The other known piscivorous species, *C. catus* and *C. obscurus*, were not collected by the writer on reef platforms, but

TABLE 15. Food of Molluscivorous Species of *Conus* on Reefs.

	C. pennaceus	*C. marmoreus*		*C. textile*	
	All Reefs	All Reefs	Total	All Reefs	Total
No. Specimens Examined...	146	3	7	2	10
Haminoea crocata Pease	24	—	—	—	—
Haminoea sp. cf. *H. aperta* Pease	2	—	—	—	—
Haminoea sp. 1057	1	—	—	—	—
Phasianella variabilis Pease	12	—	—	—	—
Dolabrifera olivacea Pease	7	—	—	—	—
Gastropod sp. 1963	4	—	—	—	—
Gastropod sp. 1964	4	—	—	—	—
Trochus intextus Kiener	3	—	—	—	—
Turbo intercostalis Menke	2	—	—	—	—
Pleurobranchus sp. 1064	2	—	—	—	—
Gastropod sp. 988	2	—	—	—	—
Natica marochiensis Gmelin	1	—	—	—	—
Conus abbreviatus Reeve	—	1	3	—	—
Conus lividus Hwass *in* Bruguiere	—	1	2	—	—
Conus sp.	—	—	1	—	—
Conus pennaceus Born	—	—	—	1	1
Conus striatus Linne	—	—	—	—	1
Morula ochrostoma Blainville	—	—	—	—	1
Unidentified Gastropods	7	—	—	—	3
Total Gastropods	71	2	6	1	6
Unidentified Food	23	1	1	1	1

References consulted in the identification of the mollusks in this table were Edmondson (1946), Ostergaard (1955), Pease (1860), and Pilsbry (1917, 1920).

Ostergaard (1950) reported the former species from Station 3.

SUMMARY OF FOOD AND FEEDING IN THE SUBTIDAL REEF HABITAT

Modifications of radula teeth which can be correlated with increased frequency of feeding on tube-dwelling polychaetes are present in many of the vermivorous species of *Conus* characteristic of the subtidal reef platform habitat. A forward projecting cone on the base, which may aid in retaining the tooth in the proboscis while the prey is extracted from its tube, is present in the two dominant reef species, *C. flavidus* and *C. lividus*. The former preys almost exclusively on tube-dwelling Terebellidae. Polychaetes preyed on by *C. lividus* are chiefly terebellids, but the dominant food species is the enteropneust *Ptychodera flava*. In addition to the basal cone, both *C. flavidus* and *C. lividus* possess a backward projecting spur on the shaft of the radula tooth, about one-third of the length from the base. Peile (1939) suggested that this structure may serve to prevent the tooth from being forced back into the proboscis on the impact of the sting.

The chief differences in the radula teeth of *Conus lividus* and *C. flavidus* are that the latter is shorter and is finely serrate (in disagreement with Peile 1939), while the former has a long shaft and no serrations. There is no obvious adaptive significance to these differences; nevertheless, the difference in nature of the food of the two species is highly significant ($P < 10^{-6}$).

The characteristics of the radula teeth of *Conus*

sponsalis, C. abbreviatus, C. ebraeus, and *C. rattus* were discussed above. Differences in the feeding habits of these species on reef platforms are apparent from inspection of Table 13. The feeding habits of *C. abbreviatus* and *C. rattus* are most similar to each other, but even these differ highly significantly ($P = 10^{-6}$) in the samples examined.

Conus imperialis, C. miles, C. vexillum, and *C. vitulinus* all possess the forward projecting cone on the base of the radula teeth. All feed primarily on polychaetes which either burrow into coral (Eunicidae) or live under rocks or in crevices (*Eurythoe*). The presence of the cone is therefore correlated with the habit of feeding on burrowing polychaetes, and it may well serve the function of aiding in the extraction of the worm from its tube, as suggested by Peile (1939). Distinct differences in the nature of the food of all of these species is also apparent from Table 13, although the samples are rather small for rigorous statistical analysis.

Conus distans, which also feeds on burrowing eunicids, does not possess the basal cone on the radula tooth, but the terminal knob is extremely large and may have the same function. The food of *C. distans* is similar to that of *C. rattus,* but the differences between them are highly significant ($P < 10^{-3}$).

On reef platforms as on marine benches, the nature of the food of each vermivorous species of *Conus* differs significantly from that of all other species. Thus these species avoid competition for food among each other. In addition, they are completely ecologically isolated, with respect to food, from *C. pennaceus,* which feeds only on a large number of other gastropods. Two other molluscivorous species, *C. marmoreus* and *C. textile,* occur only very rarely on reef platforms. *C. striatus* is the only piscivorous species collected by the author on the reefs, although small numbers of *C. catus* also occur in this habitat.

Amount of Food Eaten

Thorson (1956) has recently called attention to the need for more information on the quantity of food consumed by predators in order to understand the dynamics of benthic communities. A few data on predatory benthic fishes show that the daily food consumption is equal to 3-5% of the weight of plaice (Dawes 1930, 1931). Smith (1950) calculated rates of 1.1-2.4% in benthic fishes of Block Island Sound. Among the gastropods, young, growing specimens of *Polinices duplicata* Say, feeding on *Gemma gemma* Totten, consumed about 7% of their own weight per day. The rate in older *Polinices* was about 5% (Turner 1951). Higher rates of 10-25% were calculated for other predatory gastropods by Thorson (1958).

In the data on *Conus* which follow, dry weight of the predator (excluding shell) is compared with dry weight of the prey. Dry weights of *Conus* were measured following heating at 100°C for 48-96 hr, or by estimation from "alcohol weight" using the conversion given by Holme (1953). Dry weights of polychaetes were determined by the method of Holme.

Enough specimens of *Perinereis helleri* were available to establish the relationship between maxilla length and body weight. Thus the weight of the prey organisms could be determined even if only the maxillae were found in the alimentary tract of the predator. Using data obtained with this method as well as from direct weighing of intact polychaetes found in crops, the amount of food (17 *P. helleri*) consumed by 17 adult *Conus ebraeus* was calculated to average 0.0049 ± 0.0005 g. Dry weight of the predators was 0.43 ± 0.02 g. Since the daily feeding rate was estimated to be one polychaete per snail, the daily food consumption of *C. ebraeus* is equal to about 1% of its own body weight. Average quantitative food consumption of the four dominant species of *Conus* on marine benches, in per cent of body weight per day, was:

C. sponsalis	4.6%
C. abbreviatus	3.4%
C. chaldaeus	1.2%
C. ebraeus	1.2%

The two smaller species consume proportionately more food per day than the larger species. The rates are somewhat lower than those cited above for other predatory gastropods. The reason is probably that all of the other figures are for temperate species, many of which do not feed in winter. Since the time available for feeding is shorter, the feeding rate during the season is likely to be higher than in a tropical gastropod such as *Conus,* which feeds at a constant rate throughout the year.

PREDATION ON *CONUS*

The extent of predation on *Conus* is difficult to evaluate. In the course of collecting trips, freshly dead fragments of *C. catus, C. rattus, C. abbreviatus,* and *C. flavidus* were observed on marine benches. In some cases, shells had been broken into many pieces so recently that most of the pieces were present within a few square centimeters. On reef platforms, shell fragments of freshly killed specimens of 11 species of *Conus* were collected. Fragments of the relatively thin-shelled *C. pennaceus* were found most often. Surprisingly, fragments of the extremely thick-shelled *C. flavidus* were second commonest. These cases are believed due to predation. The identity of the predators is not known, but parrot fishes (Scaridae) and the zebra eel, *Echidna zebra* (Shaw) are possibly responsible.

Other organisms, including the other species of *Conus* mentioned in the previous section, other gastropods (*Cymatium*), and starfish (*Asterope*), were observed to prey on *Conus* in the laboratory.

Cymatium nicobaricum Röding readily attacked *Conus* in laboratory aquaria. A large specimen (shell length 84 mm) devoured specimens of *C. ebraeus, C. abbreviatus,* and *C. catus.* Dead *C. ebraeus* were also eaten. In one case, a live *Conus ebraeus* was attacked by *Cymatium nicobaricum* about 20 min after the two

were placed in the same aquarium. The predator introduced its proboscis into the aperture of the *Conus* shell, and apparently began to rasp off pieces of the foot with its radula. This position was maintained for 9 days, after which the empty *Conus* shell was released. *Cymatium,* which is represented by several species in Hawaii, is a likely predator of *Conus* in nature.

Although specimens of the starfish *Asterope carinifera* Lamarck were kept for months in aquaria with several species of *Conus,* predation was observed only rarely. It is not known whether *Asterope* preys on *Conus* in nature. The starfish is not very common, and its habitat is often not shared by *Conus.* Both *Asterope* and *C. ebraeus,* which the starfish ate in the aquarium, were however found at Station 13.

Xanthid crabs also attacked *Conus* in laboratory aquaria. The attacks usually resulted in the outer lip of the shell being broken off. Crabs were never observed to succeed in killing the gastropods, probably because the latter could retract farther into the shell, and the older portions of the shell were too thick for the crabs to break. However, laboratory observations were made only on two thick-shelled species, *C. lividus* and *C. flavidus.* Crabs may prey more successfully on some of the thinner-shelled species.

Two species of fishes, a wrasse, *Stethojulis axillaris* (Quoy and Gaimard) and a goby, *Chlamydes cotticeps* (Steindachner), were reported by Strasburg (1953) to feed on the eggs of *Conus* in Hawaii. The problem of predation on larvae remains unstudied. Large numbers of free-swimming veligers are undoubtedly consumed by carnivorous planktivores. Many newly settled larvae probably fall prey to brittle stars (*Ophiocoma* spp.) which abound on the reefs.

FOOD CHAINS AND TROPHIC STRUCTURE OF THE COMMUNITY

The polychaetes on which the dominant marine bench species of *Conus* feed are mainly herbivorous. At Station 5, *Perinereis helleri* was found to feed chiefly on the blue-green alga, *Lyngbya majuscula.* Alimentary tracts of specimens collected at night were often full of the filaments of this alga. Eunicids also feed on *Lyngbya* as well as on other algae .

Since predation on adult *Conus* may be assumed to be negligible, a short food chain of three steps is indicated. Since the numbers of species at the two higher trophic levels are large, increased efficiency associated with a restricted diet can be achieved without detracting from community stability (MacArthur 1955).

Data presented above for biomass of polychaetes and *Conus,* together with dry weights of algal samples collected about halfway across the bench at Station 5, were used to calculate the biomass pyramid for the algae-polychaete-*Conus* food chain shown in Fig. 28. The dominant alga in the sample was *Laurencia* sp. Since this does not appear to be eaten by the polychaetes under discussion, only *Lyngbya majuscula,* which represented 7% of the algae sample, is included in the pyramid.

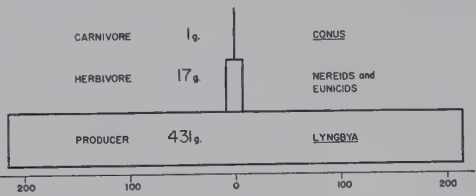


FIG. 28. Pyramid of biomass for the algae-polychaete-*Conus* food chain at Station 5.

For this food chain, the ratios of standing crop between trophic levels are herbivores/producers 4% and carnivores/herbivores 6%. It is to be noted that these ratios apply only to the single food *chain* considered and not to the entire community or food *web.*

ECOLOGICAL NOTES ON OTHER SUBTIDAL HABITATS

The most important habitats of *Conus* in the Hawaiian Islands are the intertidal marine benches and subtidal reef platforms which have been discussed in the previous sections. The relatively fragmentary ecological information which has been gained concerning species which occur chiefly in other habitats is summarized in the following paragraphs.

Conus quercinus. Certain limited regions off the shore of Oahu, usually in bays, are characterized by vast areas of sand substratum uninterrupted by coral heads or limestone outcrops. Wave action is usually comparatively light, and the salinity is often somewhat reduced by the proximity of streams. Portions of such areas may be a foot or two above the 0 tide datum, forming a sand spit. Station 2A, Sand (Ahuolaka) Island, in Kaneohe Bay (Fig. 4), is such a formation. The habitat of *C. quercinus* appears to be restricted to areas of this type, at least at certain seasons. The writer's observations are in agreement with those of Bryan (1915), who stated "they (*C. quercinus*) appear to prefer the muddy brackish water conditions at the harbor mouth to a life on the coral reef in the open sea." The species is often common where it occurs, but its distribution in shallow water is probably limited by the sparse occurrence of favorable habitats about the Hawaiian Islands and by seasonal differences in habitat.

Collections made by the writer confirmed a marked seasonality of *Conus quercinus,* which had been verbally reported to him by a number of collectors. Collecting trips to Station 2A made by the writer between July, 1954, and June, 1956, are noted by closed circles in Fig. 29. A marked seasonal fluctuation in abundance, with maxima annually in February and March, is apparent. Since no quantitative sampling of the area was done, the absolute amplitude of the maxima is not meaningful.

The biological significance of the fluctuation in numbers of *Conus quercinus* is in reproduction.

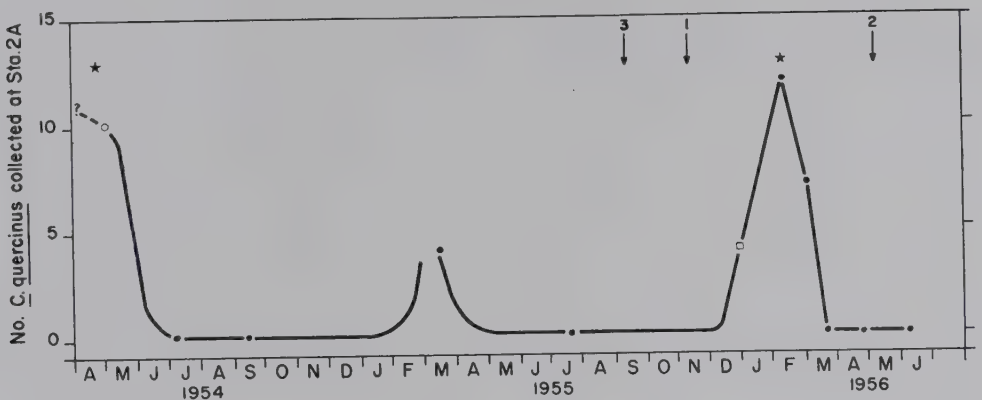


FIG. 29. Seasonal changes in abundance of *Conus quercinus* at Station 2A. Stars indicate observation of spawning of *C. quercinus* at Station 2A (1956) or in laboratory soon after being collected at Station 2A (1954). Closed circles indicate collecting trips by the author. Additional trips, during which no *C. quercinus* were seen, were made in August, 1954, and August, September, November, and December, 1955, but the exact dates were not recorded.

Explanation of vertical arrows: 1. Collection of one specimen in sampan channel, Kaneohe Bay, depth 10 ft, by A. H. Banner. 2. Collection of two specimens off Barbers Point, depth 160 ft, by R. Sheats. 3 Collection of two specimens in Bay ½ mile south of Hapuna Beach, Hawaii, depth 15-20 ft, by R. A. McKinsey.

Spawning was observed at Station 2A in February, 1956. A number of specimens collected at Station 2A in April, 1954, by staff members of the Hawaii Marine Laboratory, spawned in laboratory aquaria late the same month. The population apparently migrates to Station 2A from deeper water in early spring for spawning. The egg capsules are typically attached to the alga, *Acanthophora orientalis*. The adults then presumably return to deeper water. Specimens at Station 2A were collected in 2-10 ft of water and were most abundant in 2-5 ft. Other, "out of season" collection records from deeper water are also noted in Fig. 29.

Analysis of alimentary tract contents of 34 specimens of *Conus quercinus* revealed the commonest prey organism to be the enteropneust, *Ptychodera flava*, remains of which were found in 13 specimens. Two specimens contained remains of the sabellid polychaete, *Sabellastarte indica*. These were the only identifiable prey organisms. *Ptychodera flava* was extremely abundant at Station 2A; densities of several individuals per square foot were not uncommon.

Conus leopardus. The habitat of *Conus leopardus* is similar to that of *C. quercinus*, but the former species usually occurs in somewhat deeper water. It is rarely collected at depths of less than 10 ft. The deepest record known to the author is a specimen collected in 120 ft off Pearl Harbor, Oahu, by R. Sheats on 2 February 1956. Sand is the typical substratum, but specimens are also found on mixed sand-rubble bottoms.

No definitely identifiable food organisms were found in alimentary tracts of ten specimens which were examined. Remains in one specimen were tentatively identified as *Ptychodera flava*. The feeding of *C. leopardus* on *P. flava* was observed in the laboratory. Within a few seconds after the enteropneust was introduced into an aquarium containing a *C. leopardus*, the latter became active, extending its siphon and waving it about in the water. Several minutes later, the orange rostrum extended and began to engulf the *Ptychodera*. At no time was the proboscis visible. The prey was apparently never stung, since rhythmic contractions of the proboscis, collar and trunk regions persisted until engulfment was complete, some 18 min later.

Conus leopardus is the largest species of the genus in Hawaiian waters, the shell lengths of some specimens exceeding 200 mm. However, its radula and venom apparatus are extremely poorly developed. The radula teeth of a 160-mm specimen measured only 0.9 mm in length, comparable to those of an adult (40-mm) *C. lividus*. It is just possible that the radula, which is an extremely specialized apparatus in other species of *Conus*, is vestigial in *C. leopardus*. It must be recalled however, that some species with well developed radula teeth do not always sting the prey prior to feeding.

Conus moreleti. No identifiable food organisms were found in alimentary tract contents of 6 specimens of *Conus moreleti* which were collected in depths of 10-40 ft off the leeward (west) coast of Oahu. However, this species, which is rather similar to *C. lividus*, is probably vermivorous.

Conus obscurus. Nine specimens collected at depths of 15-35 ft off leeward Oahu were examined. Remains of an unidentified fish were present in one. Attempts to observe the feeding process in the laboratory were not completely successful. Introduction of a fish into the vessel with the snail usually evoked

extension of the proboscis. In only one instance was a radula tooth ejected, however. The fish, a specimen of *Bathygobius fuscus,* escaped and was not swallowed but died a few minutes later, presumably from the effects of the venom.

Conus textile. Specimens were collected rarely on the reefs and at depths of 10-75 ft. Results of alimentary tract examinations are included in Table 15.

Conus miles. This species occurs occasionally on reefs and benches but is somewhat more common in deeper water. Individuals on reefs are usually larger, however. Specimens collected in 35-40 ft off leeward Oahu were found to have fed on *Lysidice collaris.* (Most of the specimens of *C. moreleti, C. obscurus, C. textile* and *C. miles* discussed in this section were collected by R. M. Gray, R. A. McKinsey and C. M. Stidham.)

DISCUSSION: ECOLOGICAL NICHES AND ECOLOGICAL ISOLATION

Odum (1953) satisfactorily defined ecological niche as "the position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior." The ecological niche is multidimensional.

In the preceding sections of this paper, the species of *Conus* inhabiting Hawaiian coral reefs and marine benches have been compared with respect to some of the dimensions of niches. The purpose of this discussion is to state concisely all comparative data. From these data, evidence of ecological isolation, or its reciprocal, the overlap of ecological niches, will be evaluated.

Formulation of the theory that ecological isolation is the result of interspecific competition is due to Volterra (1926; see also D'Ancona 1954). Since Gause (1934) clearly showed that this theory was applicable to experimental populations, the postulate that in a stable community each species occupies a different ecological niche and that two or more species with the same ecological requirements cannot coexist has become known as Gause's principle (Odum 1953), Gause's hypothesis (Gilbert, Reynoldson & Hobart 1952), or, more properly, the Volterra-Gause principle (Hutchinson 1953). In such experiments, only one species finally survives in a population by inhibiting the population(s) of the other species initially present more than its own.

Although the process of competition can thus be observed in experimental populations, it is very difficult to do so in natural populations. The reasons for this are that (1) if the process occurs in nature, its rate may be very slow, and (2) it is often difficult to make the necessary determination of the behavior of a species in the absence of its presumed competitor in completely natural populations. It should be pointed out that the demonstration of niches which overlap with respect to one or more dimensions does not prove the occurrence of competition. This seems to have been overlooked by some authors (e.g. Test 1945, Odum 1953). In its most satisfactory definition, competition requires common exploitation of a limited requisite. Furthermore, mechanisms by which even species whose niches overlap with respect to limited requisites can avoid severe competition have been pointed out by Hutchinson (1953). Severe competition is used here to mean competition leading to the elimination of the less successful species.

Despite the inherent difficulties, interspecific competition has been observed in nature, particularly in birds, on a few occasions (Mackenzie 1950, Pitelka 1951, S. D. Ripley, verbal communication). The rarity of such cases, together with the invocation of other factors, led Andrewartha & Birch (1954) to a general theory of population ecology without introduction of the concept of competition. A number of studies of natural populations containing ecologically similar species provide strong evidence of a less direct sort in favor of the operation of interspecific competition in nature. Additional evidence has been derived from studies of geographical replacement of species with "too slight ecological dissimilarity" (Svärdson 1949a, 1949b).

In all carefully studied stable populations containing two or more ecologically similar species, more or less subtle differences in the ecological niches of these species have been elucidated, thus demonstrating the validity of the Volterra-Gause principle in nature. Ecologically *similar* species are just that and not ecologically *identical.* It can be stated with Gilbert *et al.* (1952), that these observations support the hypothesis that "in a population of a species, mechanisms which reduce competition between it and populations of other species tend to persist."

In the experimental studies of the Volterra-Gause principle, avoidance of interspecific competition was shown to be the result of such competition. In many natural populations ecologically similar species coexist because of reduction or avoidance of competition. In this way, the evidence from natural populations favors the hypothesis that the process of competition, leading to the avoidance of competition, operates in nature, most probably as a selection pressure.

This evidence has been derived from studies of natural populations which contain ecologically similar species of many kinds, including flatworms (Beauchamp & Ullyott 1932), fruit flies (Da Cunha, Dobzhansky & Sokoloff 1951), copepods (Hutchinson 1951), mollusks (Test 1945), fishes (Daiber 1956), amphibians (Dumas 1956), birds (Lack 1945, 1947), and mammals (McCabe & Blanchard 1951, Johnson 1943).

Except for a few papers which consider only one dimension of the ecological niche, e.g. zonation (Fischer-Piette 1935, Eslick 1940), the work of Test (1945) is the only previous such study of marine gastropods known to the writer. It deals with herbivorous limpets, of the genus *Acmaea.* Test's work differs from most of the others listed, and is more similar to the present study, in that it deals with

TABLE 16. Summary of Ecological Characteristics of Species of *Conus* on Marine Benches.

	sponsalis	*abbreviatus*	*ebraeus*	*chaldaeus*	*rattus*	*catus*
Relative abundance at all bench stations	1	2	3	4	5	6
Population density on a solution bench (Sta. 5) (no./100 sq. ft.)	0.41	0.66	1.02	0.15	0.02*	0.00
Population density on a water-leveled bench (Sta. Kl) (no./100 sq. ft.)	0.48	0.85	0.55	0.18	0.09	0.24
Population density at abrasion ramp stations* (no./100 sq. ft.)	0.25	0.21	0.00	0.07	0.33	0.00
Distance from shore of density peak at Sta. 5 (% distance across bench)	8%	8%	50%	73%	——	——
Distance from shore of density peak at Sta. Kl (% distance across bench)	22%	18%	26%	48-70%	47%	53%
Per cent of population on substratum of algal turf on bench, binding ± sand	90%	65%	65%	45%	62%	(45%)
Per cent of population on sand patches on bench	5%	26%	15%	28%	11%	(18%)
Per cent of population exposed to air at low tide	55%	35%	29%	32%	17%	29%
Per cent of population partly buried in substratum during day	30%	63%	31%	42%	10%	(44%)
Ability to withstand strong water currents (exp't'l.) (arbitrary units)	+	+	++	+		
Active period in nature and in laboratory	All species actively crawl about at night, are quiescent during day					
Per cent of diet represented by Nereidae	52%	26%	93%	85%	50%	Eats Only
Per cent of diet represented by Eunicea	44%	69%	6%	15%	50%	Fish

*Calculated from time-relative density.

more than two ecologically similar sympatric species. As many as 17 species of *Acmaea* coexist in a broad region of the California coast. Test was able to show diversification of the ecological niches of these species, despite the demonstration of varying degrees of overlap in one or more dimensions of the niches. Only quite recently have similar studies been extended to large numbers of sympatric species in other groups, namely insects (Cooper & Dobzhansky 1956; Da Cunha, El-Tabey Shehata & de Olivera 1957) and birds (Betts 1955).

A total of 18 species of *Conus* were collected by the writer on Hawaiian coral reefs and marine benches. Of these, 16 were collected on reefs and 13 on benches, dispersed among these habitats as previously discussed. On marine benches, 6 of the 13 species present are characteristic of the habitat, and only these are included in the following discussion of ecological niches. Of the others, two represent unique collection records, and five are occasionally found on benches but are more typical of the reef habitat. The factors which probably limit their abundance on benches have been discussed above.

The ecology of the species of *Conus* inhabiting marine benches is complicated by the fact that the whole life cycle is not passed in the same habitat. Recruitment of all species is predominantly from pelagic veliger larvae which are washed onto benches from other areas of origin, particularly subtidal reefs, where conditions for spawning are more favorable.

The ecological requirements of pelagic larvae and newly metamorphosed young are unknown and are extremely difficult to study. Because of their small size, newly settled larvae are virtually impossible to observe in nature. Attempts to raise young from eggs in the laboratory generally failed. Veligers usually hatched and swam about freely but died before settling to the crawling mode of life. The food at these early stages is unknown. Veligers are probably plankton or seston feeders. It is not known whether or not newly settled larvae immediately assume the carnivorous habit, or at what stage the venom apparatus becomes functional.

Requisites which govern population density of pelagic veligers and newly-settled young stages may affect the observed adult population densities reported here. Predation may well be an important factor. These statements are, however, not based on positive evidence. The hypothesis was not amenable to investigation in the time available, so adult populations only were studied. The evidence to be summarized in Tables 16-20 suggests that adults of all species studied are sufficiently isolated ecologically that interspecific competition does not limit population densities.

In Table 16, all characteristics of ecological niches studied are summarized for the six most abundant species of *Conus* on marine benches. All of these species also occur in the subtidal reef habitat, although usually in considerably lower abundance. In Table 17, data for the 8 most abundant species on subtidal reefs are similarly summarized.

In order to determine the significance in niche differentiation of interspecific differences with respect to dimensions of niches, the results of statistical analyses of all observed ecological data relating to these species are sumarized in Tables 18-20. In the right column of these tables the category of relationship of *Conus* to a number of environmental factors is listed. The statistical test applied to the data and the probability of the samples of the two species having been drawn at random from the same population are given in the second and third columns, respectively. Probabilities in most cases are extremely low. However, it is not legitimate to attribute all

TABLE 17. Summary of Ecological Characteristics of Species of *Conus* on Subtidal Reefs.

	flavidus	*lividus*	*pennaceus*	*abbreviatus*	*ebraeus*	*sponsalis*	*rattus*	*imperialis*
Relative abundance at all reef stations	1	2	3	4	5	6	7	8
Population density on a reef platform (Sta. K3) (no./100 sq. ft.)	0.03	—	—	0.07	0.09	—	—	—
Per cent of population on sand substratum	56%	64%	75%	78%	61%	38%	22%	48%
Per cent of population on reef limestone substratum	26%	22%	21%	13%	20%	30%	38%	26 %
Per cent of population on coral, rubble and rough coral bench substrata	18%	14%	4%	4%	19%	23%	40%	26%
Dominant component of particulate sediments	coarse+very coarse sand		coarse sand	coarse+very coarse sand				fine to coarse sand
Per cent of population buried or under rocks during day	15%	10%	100%	54%	27%	13%	14%	8%
Per cent of diet represented by Nereidae	—	—	—	—	15%	46%	23%	—
Per cent of diet represented by Eunicea	—	12%	—	100%	82%	50%	77%	27%
Per cent of diet represented by Terebellidae	64%	14%	—	—	—	—	—	—
Per cent of diet represented by all polychaetes	96%	39%	Eats only Gastropods	100%	100%	100%	100%	100%
Per cent of diet represented by enteropneusts	4%	61%	—	—	—	—	—	—

of the differences solely to the dimensions of the niches. If the degree of overlap is large, chi-square (but not Wilcoxon) tests may indicate significant differences if the sample also is large. A hypothetical case is illustrated in Fig. 30. In both both A and B, the probability that the two samples were drawn at random from the same population is the same. The ecological significance of the two situations is, however, quite distinct. Because of differences in position of the curves on the abscissa, competition between N_1 and N_2 for the requisite represented is much less likely in B than in A. Competition does not necessarily take place in either case.

For this reason the degree of overlap of the species with respect to each dimension is also included in Tables 18-20. In entries where the interspecific differences are highly significant, and where per cent overlap is large, the biological significance is less than the low probabilities might imply. That is, the possibility of competition is not virtually precluded.

Inspection of Table 16 shows as a first approximation that *Conus sponsalis* and *C. abbreviatus* are ecologically more similar to each other than to the other species in the table. These species are also similar in absolute abundance and in size. They are closely related systematically, usually being placed in the same subgenus (*Virroconus*). The results of statistical analyses of all observed ecological data relating to these two species are summarized in Table 18. Population densities are similar at the two most thoroughly studied bench stations, but they differ significantly when all marine benches are considered. The great difference in abundance on different reefs is due to the fact that *C. sponsalis* is much more abundant than *C. abbreviatus* at Station 7 and less abundant at all other reef stations. Both species are almost identically distributed over the benches where both are abundant. Despite the fact that both are common in the same habitat, the two species differ at the 1% level of significance with respect to all other dimensions of the

TABLE 18. Statistical Analyses of Ecological Data: Comparison of the Ecological Niches of *Conus sponsalis* and *C. abbreviatus*.

Relation of *Conus* to Environmental Factor	Statistical Test	P	Per cent Overlap
1. Relative abundance at Stations 5 and K1	Chi-square	.8	95%
2. Relative abundance on three types of benches	Chi-square	<.01	53%
3. Relative abundance on four reefs	Chi-square	$<10^{-6}$	14%
4. Distribution pattern on a solution bench (Sta. 5)	Wilcoxon	≫.05	80%
5. Distribution pattern on a water-leveled bench (Sta. K1)	Wilcoxon	≫.05	80%
6. Occupation of different types of substratum on marine benches	Chi-square	<.001	62%
7. Occupation of different types of substratum on reefs	Chi-square	10^{-5}	42%
8. Frequency of burrowing into substratum during day: marine benches	Chi-square	<.01	50%
9. Frequency of burrowing into substratum during day: reefs	Chi-square	≪.001	42%
10. Frequency of exposure to dry air at low tide on marine benches	Chi-square	<.01	67%
11. Nature of food: Frequency of Eunicea and Nereidae eaten on marine benches	Chi-square	<.001	59%
12. Nature of food: Frequency of individual prey species on benches	Chi-square	10^{-6}	42%
13. Nature of food: Frequency of Eunicea and Nereidae eaten on reefs	Chi-square	≪.01	34%
14. Nature of food: Frequency of individual prey species on reefs	Chi-square	$<10^{-6}$	25%
15. Food preference in choice experiments	Chi-square	<.001	48%

Entries 8, 10, and 11, are dependent on 7, 12, and 13, respectively.

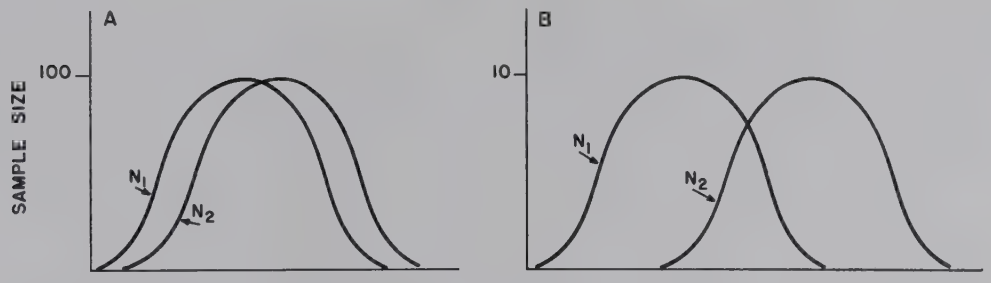


FIG. 30. Hypothetical case indicating the possibility of interspecific competition despite apparent statistically significant difference in niches. Explanation in text.

ecological niches which were investigated. Furthermore, the degree of overlap is small, hence ecological isolation is pronounced, with respect to all other factors.

Conus ebraeus and *C. chaldaeus* are the two species which are most closely related systematically. Both belong to the same subgenus (*Virroconus*) as *C. sponsalis and C. abbreviatus*. Many authors have considered *C. chaldaeus* to be a variety of *C. ebraeus*. This view has persisted among a few recent workers (e.g. Dodge 1953). Usually, however, both are accorded specific rank, and even opponents of this view have acknowledged the absence of intergrades. In Hawaii, the shells of these two species are quite distinct in appearance, much more so than in other parts of their range (Kohn unpublished.).

Furthermore, evidence discussed above and summarized in Table 19 indicates that the microhabitats of *Conus ebraeus* and *C. chaldaeus* are quite distinct, although the two species are typically found together in the marine bench macrohabitat. Since *C. ebraeus* is fairly common on reef platforms, but *C. chaldaeus* is virtually excluded, all of the comparisons in Table 19 are concerned only with marine benches. There the relative abundance, relation to substratum, frequency of exposure to air at low tide, and general nature of the food are very similar. However, striking differences in pattern of distribution across benches and especially in the specific nature of the food are apparent. The degree of overlap between the niches with respect to these two dimensions is extremely small. The two species are thus able to coexist and avoid interspecific competition.

Inspection of Tables 16 and 17 suggests that *Conus ebraeus* is ecologically about as similar to *C. abbreviatus* as it is to *C. sponsalis*. A similar comparison of the ecological data of *C. ebraeus* and *C. sponsalis* was also made. These two species differ significantly from each other with respect to almost all of the dimensions of ecological niches which were studied.

TABLE 19. Statistical Analyses of Ecological Data: Comparison of the Ecological Niches of *Conus ebraeus* and *C. chaldaeus* on Marine Benches.

Relation of *Conus* to Environmental Factor	Statistical Test	P	Per cent Overlap
1. Relative abundance at Stations 5 and K1	Chi-square	.2	71%
2. Relative abundance on three types of benches	Chi-square	.03	80%
3. Distribution pattern on a solution bench (Sta. 5)	Wilcoxon	<.01	59%†
4. Distribution pattern on a water-leveled bench (Sta. K1)	Wilcoxon	<.01	14%*
5. Occupation of different types of substratum	Chi-square	.17	63%
6. Frequency of burrowing into substratum during day	Chi-square	.6	80%
7. Frequency of exposure to dry air at low tide	Chi-square	.6	94%
8. Occupation of particulate sediments with different mechanical properties	Wilcoxon	.05	75%
9. Nature of food: Frequency of Nereidae and Eunicea eaten	Chi-square	.22	83%
10. Nature of food: Frequency of individual prey species	Chi-square	$<10^{-6}$	0.5%

Entry 9 is dependent on entry 10.
†Overlap=3% if only 2nd and 3rd quartiles of the distribution shown in Figure 20 are considered.
*Overlap=0% if only 2nd and 3rd quartiles of the distribution shown in Figure 22 are considered.

Inspection of Tables 16 and 17 suggests that *Conus rattus* is ecologically quite similar to *C. ebraeus*. *C. rattus* is placed in a different subgenus (*Lithoconus* or *Rhizoconus*) from the other bench species. An analysis similar to those of Tables 18 and 19 indicated that differences with respect to several dimensions of the niches of the two species are not significant and that there is considerable overlap. However, the two species are usually not found in the same

place, for *C. rattus* dominates the abrasion ramp benches where *C. ebraeus* is absent. Where both occur, *C. ebraeus* is the more successful, judging from absolute numbers of both present on solution benches, water-leveled benches, and reef platforms. The difference between the food of these two species is also highly significant. On marine benches, the food of *C. rattus* is most similar to that of *C. sponsalis* ($P = .7$ in comparison of families of polychaetes eaten), but the individual species preyed on by *C. rattus* and *C. sponsalis* differ highly significantly ($P < 10^{-6}$), and the overlap is only 22%.

Of the species of *Conus* characteristic of marine benches, *C. catus* (subgenus *Chelyconus*) was the least abundant. This species was commonest at Station K1, where its greatest density was nearer the outer edge than any other species present (Fig. 22). Samples were too small to provide reliable information on most other characteristics of the niche. However, *C. catus* is completely ecologically isolated from all other species of *Conus* which inhabit marine benches by the nature of its food, which consists entirely of fishes.

Turning to the species characteristic of subtidal reef platforms, it is apparent from Table 17 that *Conus flavidus* and *C. lividus,* the two most abundant species, are very similar ecologically. Since both occur uncommonly on marine benches, only data from reef stations are presented in Table 20, which summarizes the comparative ecology of these two species.

TABLE 20. Statistical Analyses of Ecological Data: Comparison of the Ecological Niches of *Conus lividus* and *C. flavidus* on reefs.

Relation of *Conus* to Environmental Factor	Statistical Test	P	Per cent Overlap
1. Relative abundance on four reefs (Stations 3, 4, 7, 9)	Chi-square	.001	64%
2. Relative abundance on three reefs (Stations 3, 4, 9)	Chi-square	.08	75%
3. Distribution pattern on three reefs	Wilcoxon	$\gg .05$	88%
4. Occupation of different types of substratum	Chi-square	.15	77%
5. Association with particulate sediments with different mechanical properties	Wilcoxon	.05	42%
6. Nature of food: Frequency of major groups eaten*	Chi-square	$<10^{-6}$	12%
7. Nature of food: Frequency of individual prey species eaten	Chi-square	$<10^{-6}$	10%

*Major groups = Terebellidae, other polychaetes, and enteropneusts

On most reefs, the abundance of *C. flavidus* and *C. lividus* is similar. An exception is Station 7, where the latter species was much the more abundant. The significant difference in abundance in the first entry of Table 20 is due entirely to Station 7, as the second entry shows. The nature of, and relation to, the substratum is similar in both species. The most striking difference in the ecological niches of *C. flavidus* and *C. lividus* is in the nature of the food. Frequency differences in the samples examined are highly significant, and degree of overlap is exceedingly low. There is thus little possibility of competition for food. Extensive overlapping with respect to other environmental requisites may permit competition, however.

A number of vermivorous species occur on reefs in very low population densities. Three of these, *Conus distans, C. vexillum* and *C. imperialis,* attain a larger size than almost all of the other species found on the reefs. Specimens of *C. distans* collected ranged from 46 to 131 mm in shell length; the range in *C. vexillum* was 44-85 mm, and in *C. imperialis,* 52-88 mm. These species, as well as *C. miles* and *C. vitulinus,* feed on eunicid polychaetes. Some of these species may be restricted to eunicids for food, but *C. imperialis* also feeds on the amphinomid polychaete, *Eurythoe complanata.* Since the samples collected were small, little statistical information was obtained. However, the data presented in Table 13 suggest striking differences in the specific nature of the prey of these species and, therefore, in that dimension of their ecological niches. The factors influencing population density are not known.

Two salient features of the niche of *Conus pulicarius* serve to isolate this species ecologically from its sympatric congeners. *C. pulicarius* occurs most often in large areas of deep sand on reef platforms, while the more abundant *C. flavidus* and *C. lividus* occur most often on patches of thin sand on reef limestone, or in small sandpockets. Secondly, part of the diet of *C. pulicarius* consists of the echiuroid, *Thalassema,* which as far as is known is not exploited for food by any other species of *Conus.* Information on the ecology of *Thalassema* is not sufficient to determine whether these two aspects of the niche of *C. pulicarius* are related.

The ecological niche of *Conus pennaceus* differs qualitatively from those of the other reef species with respect to both space and food. This species typically remains under basalt or coral rocks on, or partly buried in, sand during the day. Other species are found only rarely in this microhabitat. Competition for food with the numerous vermivorous species is completely avoided, since *C. pennaceus* feeds solely on other gastropods. The two other molluscivorous species, *C. marmoreus* and *C. textile,* are exceedingly rare on the reefs. Data obtained by the author are too few to indicate the extent of overlap with respect to food. However, both *C. marmoreus* and *C. textile* feed at least partly on other species of *Conus* while *C. pennaceus* was never found to eat its congeners.

The wide variety of gastropods on which *C. pennaceus* feeds is further evidence that intraspecific competition is of much greater importance than interspecific competition to this species. For, as Svärdson (1949a) showed, dominant intraspecific pressure causes a species to approach more closely the tolerance limits of its niche. "In this case, the species may be said to go down the slopes of its adaptive peak" (Svärdson 1949a).

Both piscivorous species, *Conus striatus* and *C. catus,* are very rare on Hawaiian reefs. They are ecologically isolated from all of the other species by the nature of their food. Young *C. striatus* may feed

on fishes of similar size to those eaten by adult *C. catus,* but the food of adult *C. striatus* is much larger.

The data presented in the preceding paragraphs indicate a high degree of ecological isolation among the species of *Conus* considered. Except where otherwise noted, each marine bench and subtidal reef habitat is a homogeneous one, containing a single community of *Conus,* as evidenced by agreement with the theoretical distribution given by MacArthur (1957). Although such agreement implies non-overlapping niches, this ideal is not completely realized in nature. As MacArthur (1957) showed, however, the distribution expected if niches overlapped randomly would fit the observed data much more poorly.

Ecological isolation results from fractionation of the habitat into microhabitats which differ especially with respect to zone occupied, relation to the substratum, and, especially, nature of the food. The first factor is of much greater importance on marine benches than on reef platforms. In this manner, interspecific competition severe enough to lead to the elimination of some of the species from the habitat is avoided. Such avoidance of competition is a likely result of the process of competition itself (Park 1954). But, as has been noted, direct evidence bearing on this is difficult to obtain from observation of natural populations (see also Mayr 1948).

Pertinent evidence obtained in the present study is that mentioned in connection with *Conus sponsalis,* which sometimes occurs where the ecologically similar *C. abbreviatus* is absent. Here the microhabitat is broadened to include, for example, more extensive use of eunicids for food. Also, *C. rattus* occurs in very low densities where *C. ebraeus* is abundant, but the former is the dominant species on the abrasion ramp type of marine bench, where the latter is absent. Restriction of the vermivorous species to apparently optimal regions of their possible habitats may also indicate the efficacy of interspecific competition, in accord with Svärdson (1949a).

In summary, density-inactive factors of the environment (Nicholson 1955) permit certain species of *Conus* to occur in the marine bench and subtidal reef habitats. Hydrographic characteristics and certain properties of the substratum are likely to be important factors of this type. The number of ecologically closely related species which may occupy a habitat is proportional to the amount of fractionation into microhabitats, which may overlap but are sufficiently distinct that severe interspecific competition is precluded. The process by which these microhabitats are established may be interspecific competition.

The population density is adjusted to certain governing requisites in the environment. Some of the species of *Conus* which occur on marine benches in Hawaii are believed to be limited by the extent of sand substrata suitable for burrowing (*C. pennaceus*) or required by prey organisms (*C. lividus, C. flavidus*). Six other species on marine benches may be termed dominants in this habitat. Of these, the population size of *C. catus* may be limited by the amount of available food. Population densities of the more abundant species on reefs may also be limited by the amount of available food. Governing requisites of the other species are probably not amount of adult food, space, or predators. Factors which are effective at a pre-adult stage in the life history, which were not amenable to study, are likely to be important.

SUMMARY

The gastropod genus *Conus* has contributed to the enrichment of the number of species of epifaunal marine invertebrates in tropical regions in that it is typically represented by many sympatric species. Ecological observations on 25 species which occur in the Hawaiian Islands are reported. Most of the data concern natural populations of 18 species studied on intertidal marine benches and subtidal coral reefs which fringe much of the coastline of the Islands. Investigations on marine benches were carried out at nine stations on the islands of Oahu, Kauai, and Maui. Eight subtidal reefs on Oahu and Kauai were studied.

Conus populations on marine benches are composed chiefly of adult individuals. A stable population density of about 2.5 individuals/100 sq ft (30/100m^2) may be expected on solution benches and water-leveled benches. Mean density of a few quantitative samples on a reef was 0.16 individual/100 sq ft (2/100m^2). Although populations are much denser on marine benches, spawning is usually unsuccessful there, presumably because of the absence of protected sites for the attachment of egg capsules. Recruitment is from pelagic veliger larvae which originate elsewhere but are carried to benches in condition to settle and assume the benthic mode of life.

Four species (*Conus sponsalis, C. abbreviatus, C. ebraeus,* and *C. chaldaeus*) are usually dominant on solution benches and water-leveled benches. *C. rattus* is the most abundant species on abrasion ramp benches. *C. catus* is also a typical inhabitant of marine benches. *C. distans, C. flavidus, C. lividus, C. miles, C. pennaceus, C. nussatella, C. retifer,* and juvenile *C. vexillum* were also recorded from marine benches.

Conus flavidus and *C. lividus* are the dominant species on subtidal reefs, although at one station *C. sponsalis* was most abundant. *C. pennaceus, C. abbreviatus, C. ebraeus,* and *C. rattus* are also common. Other species recorded from reef stations were *C. imperialis, C. distans, C. chaldaeus, C. marmoreus, C. miles, C. pulicarius, C. striatus, C. textile, C. vexillum,* and *C. vitulinus.*

Values of an index of diversity, which measured similarity of species composition of different populations, differed but little in comparisons a) among the several bench stations, b) among the several reef stations, and c) between reef and bench stations. Quantitatively, however, certain species are characteristically most abundant on benches, while others are most abundant on reefs. Calculation of a measure of heterogeneity gave low values when the *Conus* com-

munities of reefs were compared among each other ($H' = .09$) and when the communities of benches were compared among each other ($H' = .19$). Comparison of summed reef populations with summed bench populations showed much greater heterogeneity ($H' = .84$).

At the most thoroughly studied bench and reef stations, number of species and number of individuals are related in a manner which agrees with the theoretical distribution expected in an adequately sampled, homogeneous community of a single habitat, where niches are non-overlapping and continuous.

Fractionation of the habitat into microhabitats was observed but, as expected intuitively, it is not complete. On marine benches, the species present are non-randomly distributed across the bench platform from shore to seaward edge. The distributions of *Conus sponsalis* and *C. abbreviatus* are similar. Those of all other species differ significantly from each other at the 5% level of probability. The number and biomass of *Conus* decreases from a maximum near the landward edge to the seaward edge.

On reef platforms, the distribution of *Conus* is characterized by patchiness, or clumping, which is correlated with the nature of the substratum. Distribution is not related to distance from shore or breaker line, except that density is low at both extremes. Over most of the reef platform, the observed distribution reflects the uniformity of water movements across the reef.

Differential association with different kinds of substratum on marine benches serves to partially distinguish the microhabitats of *Conus sponsalis* and *C. abbreviatus,* the latter occurring more often in sandier regions. This is correlated with the observation that *C. abbreviatus* burrows in the substratum significantly more often than *C. sponsalis.* Although these two species commonly coexist, only *C. sponsalis* was found on benches or parts of benches exposed to dry air for long periods at low tide.

On Hawaiian coral reefs, most species of *Conus* are most often found associated with sand, the most prevalent type of substratum. Only one species, *C. pulicarius,* is probably entirely restricted to a sand substratum. The two most abundant species on the reefs, *C. flavidus* and *C. lividus,* occur characteristically on patches of sand among solid substratum. *C. abbreviatus,* which occupies sandier regions of marine benches, is also a sand dweller on the reefs. *C. pennaceus* characteristically occurs on or partly buried in sand under basalt or coral rocks during the day but crawls about on the surface of the sand at night. Other species are not commonly found under rocks.

Mechanical analyses of sand suggested no niche diversification with respect to particle size distribution of this moiety of the substratum.

Alimentary tracts of 1,930 specimens of 24 species of *Conus* collected in Hawaii were examined. From these, 1,073 prey organisms were identified, 879 of them to species. Three groups of species within the genus *Conus* may be distinguished on the basis of the nature of the food: most species feed exclusively on worms, mainly polychaetes. A second group feeds exclusively on other gastropods, and the third group feeds only on fishes. Eleven species, *C. sponsalis, C. abbreviatus, C. ebraeus, C. chaldaeus, C. rattus, C. distans, C. miles, C. imperialis, C. vexillum, C. vitulinus,* and *C. pertusus,* feed exclusively on polychaetes. Samples of the last three named species were rather small, however. Three species, *C. lividus, C. flavidus* and *C. quercinus,* feed both on polychaetes and on the enteropneust, *Ptychodera. C. leopardus* probably feeds on *Ptychodera. C. pulicarius* eats polychaetes and the echiuroid, *Thalassema. C. pennaceus, C. marmoreus,* and *C. textile* feed exclusively on other gastropods. *C. striatus, C. catus* and *C. obscurus* feed only on fishes.

On marine benches, the vermivorous species of *Conus* prey almost exclusively on members of the polychaete family Nereidae and superfamily Eunicea. At one station, the species *Perinereis helleri* was found to be the primary food of the three most abundant species of *Conus.* This polychaete was so abundant, however, that food cannot be said to be in short supply. Interspecific competition for food is therefore not indicated. Species of *Conus* common to both habitats feed proportionately more often on eunicids on reef platforms than they do on marine benches, for nereids are uncommon in the former habitat.

The typically reef-dwelling vermivorous species feed chiefly on polychaetes and enteropneusts associated with the sand moiety of the substratum. Of the two dominant species, *Conus flavidus* eats mainly Terebellidae, and *C. lividus* eats mainly *Ptychodera.*

On marine benches, the dominant species of *Conus* eat polychaetes which feed on algae, forming a three-step food chain. Calculation of a biomass pyramid for this food chain gave an herbivore/producer ratio of 4% and a carnivore/herbivore ratio of 6%.

Predation on *Conus* was difficult to measure. Certain fishes, other gastropods, octopi, crabs and starfishes are possible predators on adults. Predation on free-swimming larvae and newly-settled young is presumably of major ecological significance, but it was not amenable to investigation. Other factors which may also govern population density of the various species are also considered.

Ecological niches, ecological isolation, and interspecific competition in natural populations are discussed briefly. The comparative ecology of the more abundant species of *Conus* is summarized in the discussion, with emphasis on the extent of ecological isolation. Statistical analyses of certain dimensions of the niches of the ecologically most similar species are presented. Limitations of simple tests of significance of differences are noted. Degree of overlap is extremely important in niche diversification.

The adult ecological niche of each species of *Conus* studied differs significantly with respect to at least two of the following characteristics: nature of the food, nature of and relation to the substratum, and

zonation or distribution pattern. The last is of particular importance only on marine benches. These differences are concluded to be the primary factors by which the ecological niches of species of *Conus* are differentiated. This is the mechanism which enables the maintenance of populations of large numbers of closely related, sympatric species of *Conus* in tropical regions.

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KINETICS OF LUMINESCENCE IN CHAETOPTERUS SLIME, AND THE INFLUENCE OF CERTAIN FACTORS THEREON [1,2]

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SEVEN FIGURES

Since the early work of Panceri (1878), luminescence of the polychaete annelid, *Chaetopterus,* has been the subject of occasional studies from various points of view, including histological as well as biochemical and physiological (cf. Harvey, '40, '52, '55, '57; Nicol, '52, '55; Sie, Chang and Johnson, '58 [3]). Light emission is associated with two types of secretory phenomena. In one type, gland cells located chiefly in the aliform notopodia liberate into the surrounding medium, via the oral groove, a luminescent slime which under favorable conditions glows with a gradually diminishing intensity for a period of some minutes. In the other type, a flash extending over a period of some seconds occurs, chiefly in the segmented posterior notopodia, without the liberation of appreciable quantities of free luminescent slime, but accompanied by the local discharge of material from certain gland cells that contain granules and that apparently constitute the photogenic tissue.

[1] Contribution number 114 of the Hawaii Marine Laboratory.

[2] Aided in part by Contract Nonr 1353(00), Project NR 165–253, between the Office of Naval Research and Princeton University. Reproduction in whole or in part is permitted for any purpose of the United States Government.

[3] The manuscript of the paper by Sie et al. was completed sooner, although the research was carried out later than that described in this paper.

As yet, no biochemical components of the light-emitting system have been isolated or identified, nor has a "luciferin-luciferase reaction" been demonstrated wherein light emission occurs on mixing, at room temperature, crude extracts of the photogenic tissue prepared in hot and cold water respectively.

The present investigation was undertaken in an effort to obtain further evidence on the nature and properties of the light-emitting system, primarily as it occurs in the free slime. Although attempts by various methods to enhance luminescence, or to restore it after decay, were either unsuccessful or of uncertain interpretation, data on the kinetics of decaying light intensity in various media, the influence of possible co-factors, and of inhibitors such as urethane and di-isopropyl-fluorophosphate (DFP) have revealed some hitherto undescribed characteristics of the system.

MATERIALS AND METHODS

The organisms studied were a variety of Chaetopterus variopedatus[4] found in small parchment-like tubes, from about two to 8 inches in length, attached to, or winding through small recesses in, the coral of Kaneohe Bay near the Hawaii Marine Laboratory. In detaching the tubes it was often necessary to chip away the coral, bit by bit, with a hammer and chisel. Placed on a layer of sand in a tray of running sea water, the worms remained healthy inside their tubes for several days.

Luminescent slime was obtained in a dark room by first draining the sea water from the tube then pressing gently to irritate the worm. Individual specimens varied greatly in the amount and brilliance of the slime that could be obtained in this manner; some specimens, if they responded at all, would emit only a dim glow visible through the walls of the tube, whereas others would repeatedly liberate an essentially clear and colorless but brightly luminous material in sufficient

[4] Kindly identified by Dr. Olga Hartman.

amounts to drain several drops from the tube into a small vial in an ice bath. As a rule, two or three drops of the luminescent fluid were caught in 1 to 2 ml of sea water, or other medium as desired in the vial.

Within one to three minutes after collecting the slime, a 0.5-ml portion was introduced by means of a tuberculin syringe into a specimen tube in a water bath of an apparatus similar to that described by Johnson and Plough ('59). The temperature of the bath remained satisfactorily constant, without thermostatic control, during a given experiment. On different days its varied with room temperature through a range of about 23° to 26°C. The specimen tube was shielded from extraneous light and so arranged that it could be exposed, by opening a shutter, to an RCA type 1P21 photomultiplier connected through an amplifying system to an Esterline-Angus automatic recorder. Because of a wide variability in initial intensities and rates of decay of luminescence, not only in specimens from different worms but also from the same individual, no attempt was made to standardize accurately the elapsed time between collecting the slime and recording its luminescence, though recording was usually begun as quickly as possible and essentially always within three minutes or less.

During the course of decaying luminescence one or more solutions could be added through a three-way syringe stopcock without exposing the specimen to extraneous light or interrupting the continuity of the record. The volumes used were such that the total volume of luminescent fluid was always exposed to the window of the photomultiplier.

RESULTS

Order of decay and influence of the medium

Luminescence of the secreted slime in a small volume of sea water diminishes rapidly at room temperature (fig. 1), showing that one or more components necessary for light emission disappears. Aeration with air or oxygen scarcely

affected the course of decaying luminescence. Vigorous stirring usually had no effect, though on some occasions it caused a momentary increase in intensity, possibly by stimulating bits of photogenic tissue shed by chance with the slime. Addition of just sufficient sodium hydrosulphite ($Na_2S_2O_4$) to use up the dissolved oxygen stopped light emission, but aeration with air or with oxygen would then restore luminescence. Thus, while oxygen is required for luminescence, it is not the component whose disappearance is responsible for the progressive decrease of luminescence in these experiments.

Although during the initial period luminescence sometimes appeared to decrease in the manner of a first order reaction, the rate of decay generally decreased as time went on and luminescence occasionally persisted as a dim glow for many minutes. Figure 1 (A) illustrates a typical curve for a specimen of slime caught in about 9 volumes of sea water. A second specimen from the same worm was similarly caught in sea water concentrated by evaporation to contain double the normal salt content, yet the kinetics remained practically the same as before (fig. 1, B). No significant change in kinetics was observed when phosphate buffered NaCl solution ("PN," consisting of equal volumes of 0.5 M NaCl and 0.25 M Na_2HPO_4–KH_2PO_4, pH 7.3) was used in place of sea water, nor was the course of decay appreciably altered by adding an equal volume of this solution during an early period (fig. 1, C). Similar results were obtained also with unbuffered 0.5 M NaCl (fig. 2, A). A freshly secreted drop of slime luminesced dimly even in 0.5 N HCl. A bright, brief flash of light occurred on addition of an equal volume of 0.5 N NaOH, and was followed by dim luminescence again. When fresh slime was added to several volumes of saturated $(NH_4)_2SO_4$ solution, luminescence decayed at a rate that was within the variability of different specimens (fig. 2, B). Unfortunately, the data do not reveal the differences in actual intensity in the $(NH_4)_2SO_4$ solution as compared to sea water, although visual observation indicated that it was considerably dimmer in the former than in the latter. In sea water, the decay rate

was greatly increased by the addition of 8 volumes of distilled water (fig. 2, C).

The foregoing observations indicate that the time course of decay is not seriously affected by some physiologically drastic changes in salt content of the medium, nor by dilution with one or more volumes of the same medium (cf. also figs. 5, 6 and 7). With respect to dilution, it will be recalled that

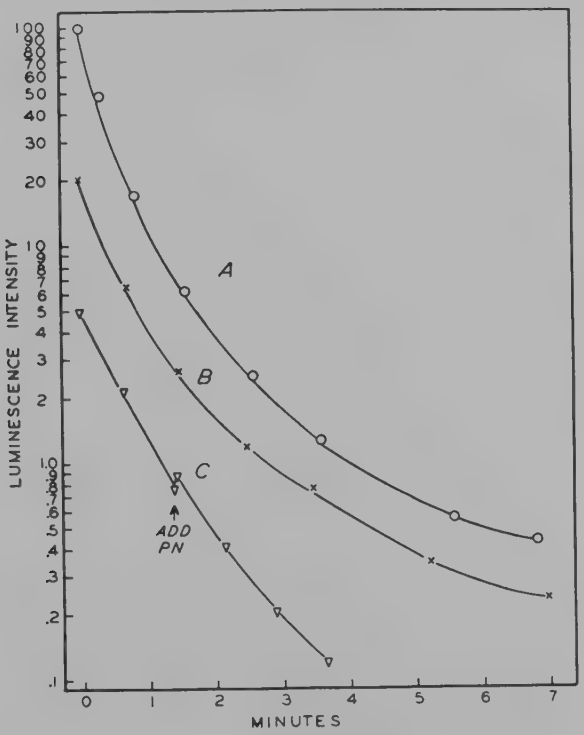

Fig. 1 Rate of decay of luminescence in Chaetopterus slime in (A), sea water (one drop of fresh slime added to 1.2 ml sea water); in (B), sea water concentrated 2 ×; in (C), phosphate-buffered NaCl solution ("PN"). Arrow on curve (C) indicates the addition of an equal volume of PN. Light intensity is in arbitrary units and each curve is arbitrarily placed with respect to the ordinate in this and succeeding figures, except figure 3.

in these experiments the total volume is kept sufficiently small that the whole solution is exposed to the photo tube. Thus, even though the brightness per unit volume decreased in proportion to dilution, the total light registered at any moment by the photo tube would not be changed by the dilution. The results obtained are similar to those of diluting a suspension of luminous bacteria. In the present instance, if the light intensity were proportional to the concentration of an enzyme in homogenous solution, the rate of decay should drop to one

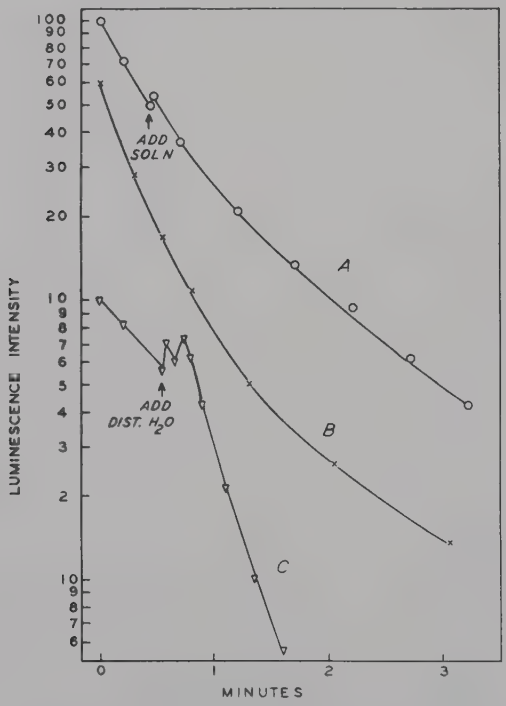

Fig. 2 Rate of decaying luminescence of slime in (A), 0.5 M. NaCl; in (B), nearly saturated ammonium sulfate; in (C), sea water. The arrow on curve (A) indicates addition of an equal volume of NaCl solution, and on curve (C), addition of 8 volumes of distilled water (3.2 ml added to 0.4 ml of slime in sea water).

half on diluting with an equal volume of the medium, or to one fourth if the intensity were proportional to the product of enzyme and substrate concentrations, except with large excess of substrate. Thus, the luminescent material in the slime behaves as if bound to, or within, particles.

Evidence concerning a possible relationship of this behavior to the granules, in presumably photogenic gland cells, revealed in histological studies of Chaetopterus (Trojan, '13; Dahlgren, 16; Krekel, '21; Hasama, '41; Bonhomme, '43; Nicol, '52), was not sought in this study. Assuming, in accordance with the results of the dilution experiments, that the reactants are indeed bound together in some manner in particulate form, the changing rate of decaying luminescence, and likewise the variation in kinetics with different specimens, could be logically attributed to an inhomogeneity of the particles. On the other hand, and possibly in addition, the observed kinetics could result from other factors, such as (1), a progressive inactivation, perhaps through thermal instability, of a critical enzyme while acting upon a more stable substrate, or (2), diffusion of a co-factor away from the enzyme, or (3), formation of reaction products that influence the catalytic activity.

With respect to the first of these possibilities, experiments on the collection and storage of the slime in saturated ammonium sulfate and in other media provided some suggestive evidence, as follows. Fresh slime mixed into cold saturated ammonium sulfate solution in an ice bath at —5 to —6°C, glowed with a dim luminescence. When quickly brought to room temperature and diluted with distilled or sea water, the light intensity increased, went through a maximum, then finally disappeared (fig. 3, A–D). The total light produced on dilution was nearly proportional to the amount of slime, while the time course was similar. The time course was changed, however, by first keeping the specimen a short while at room temperature, or for a long time in the deep freeze. At room temperature the rate of rise and fall of luminescence on dilution of the ammonium sulfate solution rapidly decreased,

resulting in a much flatter curve whose total light was difficult to compare with the preceding, but whose time to reach a maximum was lengthened. When stored in the deep freeze at —15°C, the capacity to emit light, when quickly thawed and diluted, persisted for days, but again a flattened curve resulted (fig. 3, C′). These changes are plausibly due to the inactivation of a critical enzyme, through a process that occurs

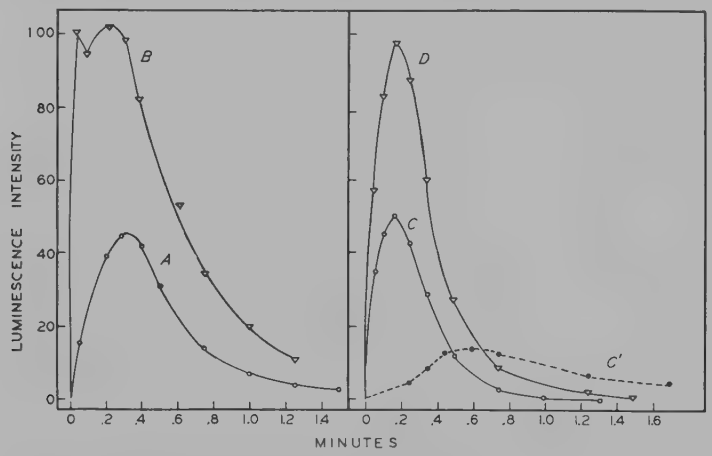

Fig. 3 Course of light intensity following addition of sea water to slime in nearly saturated ammonium sulfate. Curves (A) and (B) are from one specimen and curves (C), (D) and (C′) from another specimen. In (A), 2.9 ml sea water were added to 0.1 ml of slime; (B), 8.7 ml sea water to 0.3 ml of slime; (C), 3.4 ml of sea water to 0.2 ml of slime; and (C′), 2.4 ml sea water to 0.1 ml of a portion of the parent specimen of (C) that had been stored three days in a deep freeze at —15°C, then quickly thawed and equilibrated in the water bath.

slowly even at —15°C. It should be mentioned also that slime collected in cold sea water continued to luminesce when held at a temperature as low as —10°C. When transferred to the deep freeze, it retained the capacity for luminescence, with a similar slow rise and fall, on quickly bringing to room temperature. Whole worms placed in sea water and kept in the deep freeze would glow in certain areas for a long time after thawing, though no longer alive.

With respect to the possible role of reaction products, or diffusion away of co-factors to catalytic activity, attempts were made to determine the effects of "spent" slime on the luminescence of freshly secreted slime. Because of the variability in kinetics among different specimens of slime, con-

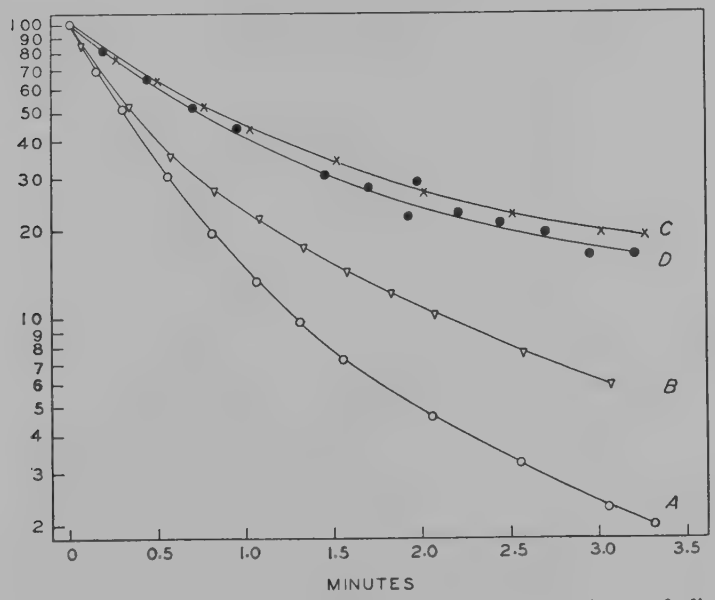

Fig. 4 Kinetics of decaying luminescence in successive specimens of slime from one individual worm, each successive specimen (B, C, D) being added to the accumulated previous specimens. The intensity at the start of recording has been arbitrarily taken as 100 in each case.

clusive results are obviously difficult to obtain. However, figure 4 illustrates the results of one experiment in which 4 successive specimens were obtained from a single individual over a short period of time, and each successive specimen was added to the previous one. Unfortunately, comparisons of initial intensities are not very meaningful; in figure 4 the intensity at the start of recording has arbitrarily been taken

as 100 in each case. Although luminescence in the first specimen decayed faster than the second, and the second faster than the third and fourth, the latter two were about the same. Since the differences in decay rates are not strictly beyond the range of normal variability it cannot be concluded that reaction products in spent slime slow the decay of luminescence of fresh slime. The results indicate the absence, however, of any reaction products in amounts sufficient to increase the rate of decay.

The addition of activated charcoal had no influence on the course of decaying luminescence, except on one occasion when there was reason to believe the sea water had been contaminated with wastes. On this occasion, the addition of small amounts of activated charcoal led to spectacular increases in light intensity.

In view of the foregoing results it appears that an important factor in the decay of luminescence at room temperature is the inactivation of an enzyme. In some instances, the process of inactivation of enzymes or denaturation of proteins has complex kinetics, being rapid at first then proceeding more slowly (cf. Johnson et al., '54), as does the decay of luminescence in the present experiments. If enzyme inactivation is the most important factor in luminescence decay of this material, the difficulty of obtaining a luciferin-luciferase reaction would be largely accounted for.

Influence of co-factors of other systems

Co-factors that are required for, or influence the intensity of, luminescence in other systems were studied with the present system by adding them to the slime both during the course and at the end of decay. Some typical results are illustrated in figure 5. Although in some instances a slight, momentary spurt of increased intensity accompanied the addition, these spurts amounted to scarcely more than those accompanying the addition of sea water alone (cf. also figs. 6 and 7), and are therefore more likely due to mechanical

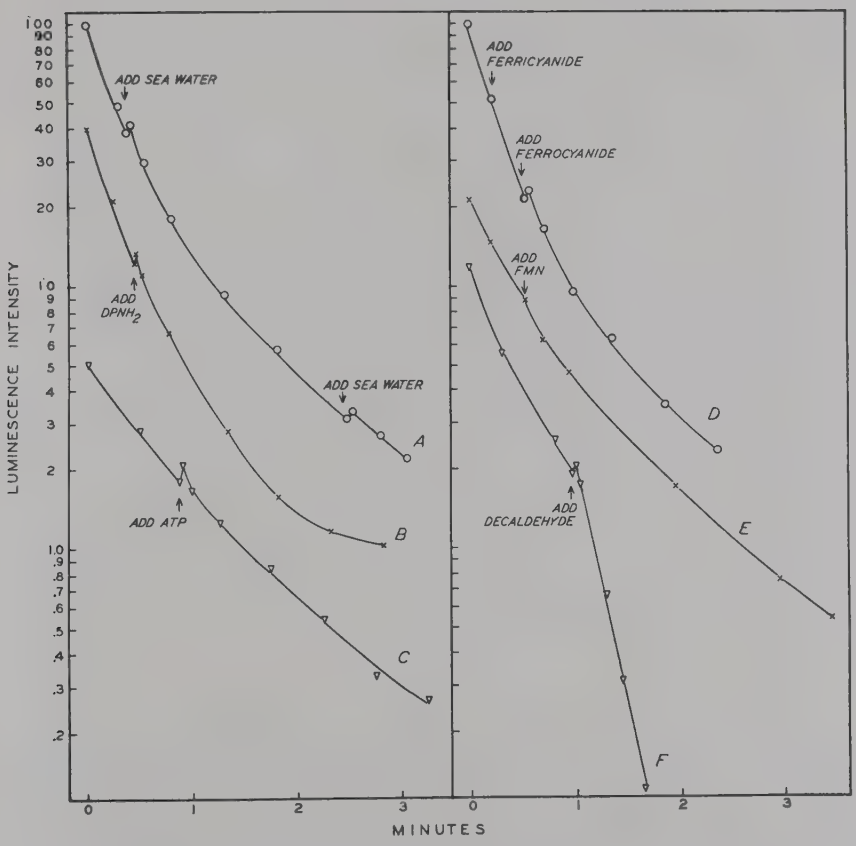

Fig. 5 Influence of adding various solutions, at times indicated by the arrows, on the course of luminescence in sea water. Curve (A), first arrow, 0.5 ml sea water to 0.5 ml slime in sea water; second arrow, additional 2 ml sea water. Curve (B), 0.5 ml sea water containing 1 mg DPNH was added to 0.5 ml of slime specimen. Curve (C), 2 mg ATP in 0.5 ml sea water, neutralized, added to 0.5 ml of slime specimen. Curve (D), 0.5 ml of 0.002 M $K_3Fe(CN)_6$ added to 0.5 ml of slime specimen (first arrow), followed by 1.0 ml of 0.002 M $K_4Fe(CN)_6$ (second arrow). Results were similar when 1.0 ml of 0.01 M $K_4Fe(CN)_6$ was added to 0.5 ml of a different specimen of slime. Curve (E), 0.5 ml sea water containing 0.02 mg FMN was added to 0.5 ml of slime specimen. Curve (F), 0.5 ml sea water containing 0.01 mg decaldehyde (obtained by dilution of 1 ml of a methyl alcohol solution containing 1 mg decaldehyde per ml with 99 ml of sea water) was added to 0.5 ml of the slime specimen.

effects than to any participation in reactions leading to light emission. With the exception of decaldehyde, which functions in light emission in luminous bacterial extracts (Strehler and Cormier, '54) but accelerates the disappearance of luminescence in the present system (fig. 5, F), the substances tested were essentially without influence. They include adenosine triphosphate (ATP), required for luminescence of firefly extracts (McElroy, '47), flavine mononucleotide (FMN) required for bacterial luminescence *in vitro* (Strehler, '53, McElroy et al., '53), reduced diphosphopyridine nucleotide which sustains bacterial luminescence *in vitro* in the presence of FMN and decaldehyde (Strehler '53, '55; Hastings and McElroy, '55), and ferro- and ferricyanide, respectively, which influence the state of Cypridina luciferin that reacts with luciferase in light production (Anderson, '36). Moreover, no combinations of FMN, DPNH and decaldehyde either retarded the decay of luminescence or restored luminescence afterwards. After the light had ceased or nearly ceased, it would not return following the addition of $Na_2S_2O_4$ and vigorous aeration, although such treatment usually results in some further light after decay of luminescence in Cypridina extracts.

Influence of urethane and DFP

Luminescence *in vitro* as well as *in vivo* has long been known to be sensitive to narcotics, and the effects of urethane on bacterial luminescence in particular have been studied at some length (Taylor, '34, '36; van Schouwenburg, '38; Johnson et al., '45, '54; Strehler and Johnson, '54). More recently, di-isopropyl fluorophosphate (DFP) has been found to inhibit the bacterial system reversibly (Johnson and Plough, '59), at higher concentrations than are required for the inhibition of specific cholinesterases in a manner that is irreversible by ordinary methods such as dilution (Bodansky, '46; Webb, '48; Koelle and Gilman, '49, Saunders, '57).

In the present study, addition of appropriate concentrations of either urethane or DFP during the course of the decay

caused a sudden drop in luminescence intensity, which was at least partially reversible on dilution. Typical data are shown in figures 6 and 7, which include also repeated examples showing the absence of any significant effect of adding one to two volumes of sea water alone. The quantitative relation between concentration of inhibitor and amount of inhibition in these experiments is subject to two sources of large error: (1), variations in sensitivity of specimens of slime from different worms or even from the same individual, and (2), the continuous change in luminescence with time, making it difficult to determine the precise extent to which the sudden decreases or increases, following addition or dilution, re-

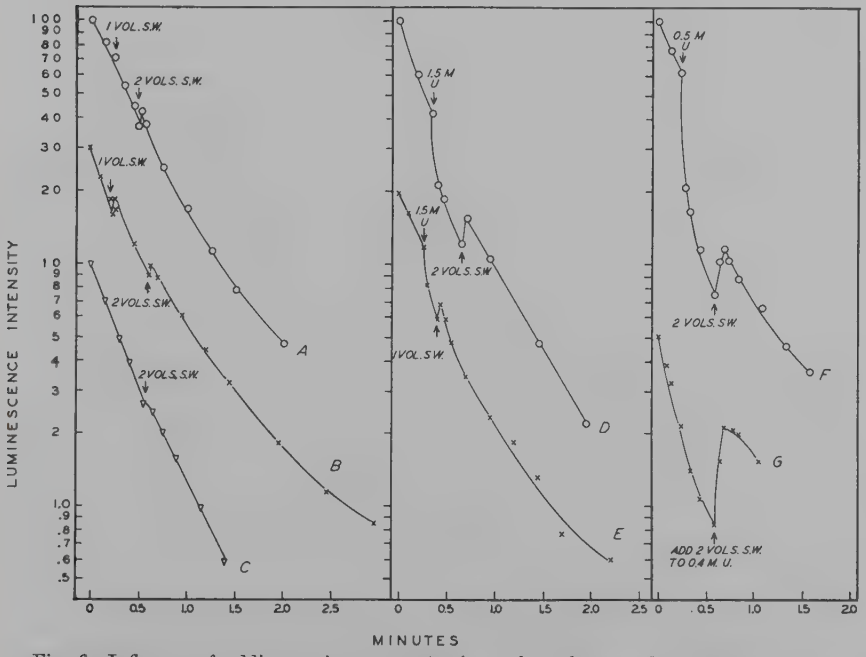

Fig. 6 Influence of adding various concentrations of urethane, and of diluting with sea water, on the course of luminescence decay of slime in sea water, as indicated in the figure. Curve (G) shows the results of adding two volumes of sea water to a slime specimen that had been added initially to a large volume of 0.4 M urethane in sea water.

spectively, measure the effects of the inhibitor. As well as could be estimated by inspection of the curves, 0.075 M to 0.25 M urethane caused sudden inhibitions ranging from 20% to 77%, and 0.002 to 0.0017 M DFP caused sudden inhibitions ranging from 28% to 71%. Averaged values from 25 experiments were plotted on a log-log scale in the manner discussed in detail by Johnson et al. ('54). In spite of some scatter of the points, the relationship for each drug appeared to be linear. The slope of the line drawn by inspection was 1.9 for the urethane inhibition and 0.8 for the DFP inhibition. These values are close to those of 2 and 1, respectively, for the same inhibitors acting on bacterial luminescence at the optimum

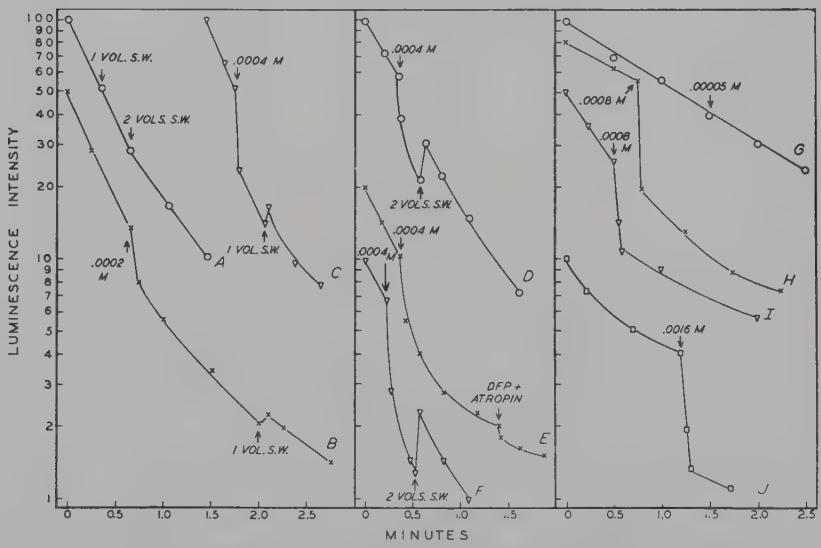

Fig. 7 Influence of adding various concentrations of DFP, and of diluting with sea water, on the course of luminescence decay. Concentrations of DFP indicated on the graph refer to final concentrations after adding 0.5 ml of the inhibitor in sea water to the slime specimen in sea water. In curve (E), a second addition consisted of DFP to give the same final concentration as the first, but in sea water containing also a final concentration of 0.003 M atropin, the well known antagonist of DFP poisoning in mammals.

temperature, and the range of effective concentrations of each drug is also similar.

DISCUSSION

From scarcely more than half a dozen of the myriad types of luminescent organisms, extending among animals from protozoa to fishes and among plants from bacteria to higher fungi, has it been possible thus far to obtain separate, cell-free extracts which emit light on mixing (Harvey, '55). Among the few of which it has been possible, sufficient biochemical information is now available with respect to three, namely, the firefly, bacterial and *Cypridina* systems, to conclude that the different enzymes are specific and the diffusible factors are not the same. Results of the present study indicate that the *Chaetopterus* system is again different, as judged by the failure of diffusible factors important in the firefly and bacterial systems, respectively, to enhance or restore luminescence of the slime. Cold water extracts of the photogenic organs of *Chaetopterus* have been found to give no visible light with *Cypridina luciferin* (Harvey, '52) or on adding ATP (Harvey, '49; Haneda and Harvey, '52).

Using the secreted slime as starting material, rather than the entire photogenic organs, a number of unsuccessful attempts were made in this study to separate components active in light emission. Although a detailed account would not seem justified, the classical method of testing for a luciferin-luciferase reaction was one of the methods tried, i.e., brightly luminous slime was quickly heated to the point that no light returned on cooling, and was then added to spent slime, but no light appeared. Some encouraging but irregular results were obtained by collecting the slime in cold acetone, filtering off the precipitate that formed and drying the acetone soluble extractives to a faintly yellowish, greasy and salty residue. When a 3% solution of this residue was added in small amounts during the course of luminescence decay of slime in sea water, large increases in light occurred in some instances

but only very slight increases in others. Wetting the residue with sea water, or adding 3% solutions of the residue to solutions of the precipitate that had been filtered out of the acetone and then dried, did not result in detectable light emission, and the dried precipitate itself gave no light when wet with sea water.

The kinetic evidence that the reactants in luminous slime are organized in a particulate manner, rather than occurring in homogenous solution, suggests that this may be an important factor in the difficulty of separating active components. The evidence for instability of an essential catalyst suggests another factor, perhaps even more important. The method, however, of using the kinetics of decay as a means of assay for the influence of various factors, and of investigating the properties of such systems as this, apart from the added complexities of physiological control, appears to offer further possibilities (cf. Sie, Chang and Johnson, '58 [3]). By appropriate refinements in technique, the slime could probably also be used satisfactorily for investigating the action of factors influencing the total, as well as instantaneous, intensity of the emitted light.

SUMMARY

The kinetics of decreasing light intensity in the luminous slime secreted by Chaetopterus variopedatus has been studied with reference to the order of decay and the influence of salt content of the medium, diffusible factors of other luminescent systems, and the inhibitory effects of urethane and DFP.

The initial rate of decay was nearly exponential, but decreased progressively, sometimes ending in a dim, long-lasting glow of luminescence.

The time course of decaying luminescence of slime in sea water was not significantly altered by aeration with air or oxygen, by addition of one or two volumes of sea water, by addition of small concentrations of FMN and DPNH, separately or in combination, or by addition of ATP. The decay

[3] See footnote 3, page 259.

rate was increased by adding small concentrations of decaldehyde or 8 volumes of distilled water.

The kinetics of decaying luminescence of slime added initially to twice concentrated sea water, to 0.5 M NaCl, to 0.25 M NaCl in 0.125 M phosphate buffer of pH 7.3, or to saturated ammonium sulphate was essentially the same as that of slime added initially to sea water. The relatively dim luminescence of slime added initially to saturated ammonium sulphate brightened on dilution with sea water, then decayed, giving a total light approximately proportional to the amount of slime, in different portions of the same specimen kept cold. Light-emitting capacity of slime mixed into saturated ammonium sulfate solution was quickly lost at room temperature, but could be preserved for days at —15°C, accompanied by a slowing of the rate of increasing intensity when quickly thawed and diluted. Quickly frozen fresh slime retained a capacity for light emission on thawing after storage at —15°C, as did whole worms.

During the course of decaying luminescence of slime in sea water, sudden decreases in intensity occurred on the addition of urethane in final concentrations of 0.075 to 0.25 M, or of DFP of 0.0002 to 0.0017 M. Sudden increases in intensity then occurred on dilution with an equal or larger volume of sea water.

Attempts by various methods to obtain, from luminescent slime, components active in light emission led to negative or equivocal results.

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The author is pleased to acknowledge the generous and effective cooperation of Dr. Robert Hiatt, Director, Dr. H. A. Banner, Associate Director, and the other members of the staff of the Hawaii Marine Station. Indebtedness is acknowledged also to Dr. Olga Hartman, who kindly identified the species of Chaetopterus, and to Mrs. Johnson and Mr. Milton Lieberman who collected and prepared the specimens.

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THE LUMINESCENT FLASH OF POLYCIRRUS [1,2]

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FOUR FIGURES

Although the histology of *Polycirrus* has been investigated in some detail (Dahlgren, '16; Tanassiicuk, '25; Bonhomme, '47, '52), data on the physiology and biochemistry of luminescence in this marine polychaete, as well as in other luminous worms of the family Terebellidae, are largely lacking. Harvey ('55) lists the luminescent system of *Polycirrus* as extracellular and dependent on oxygen, but negative (Harvey, '26) with respect to a "luciferin-luciferase reaction," wherein by definition light emission occurs on mixing a cooled hot-water extract with a cold-water extract of the photogenic organs. The system is also negative with respect to ATP, since after cessation of luminescence in photogenic tissue that has been ground with sand and water, no light appears on addition of ATP (Nicol, '54).

According to Bonhomme ('52) luminescence of *Polycirrus* involves a slow melting of granules, in one of three types of cells present in the epithelium, to a mass of material which emits light when secreted, the exact moment of luminescence being difficult to determine, but possibly accompanying hydration of granules or their dissolution in sea water. This process "se fait lentement et de facon continue ce qui concorde parfaitement avec le caractère lent, peu intense et continu de

[1] Aided in part by Contract Nonr 1353(00), Project NR 165–253, between the Office of Naval Research and Princeton University. Reproduction in whole or in part is permitted for any purpose of the United States Government.
[2] Hawaii Marine Laboratory Contribution No. 115.

la lumière émise.'' The results of the present study, dealing with characteristics of the response to electrical stimulation, show that this worm is capable of emitting a series of rapid flashes, of the order of tenths of a second in duration, in addition to slower, more continuous glows.

Polycirrus sp., used in this study, was encountered on rare occasions associated with specimens of a small Chaetopterus found on coral in shallow waters of Kaneohe Bay near the Hawaii Marine Laboratory. In the dark, luminescence in response to irritation appeared to come only from the tentacles, which extended for as much as 5 cm from a yellow body of about 0.5 cm. The light showed up as slow flashes or glows at various distances from the body, and also in tentacles that had been severed from the body.

For recording luminescence, a specimen was placed in the central chamber of a small lucite container similar to the type designed by Chang ('54), with stimulating electrodes dipping into relatively large pools of sea water in wells on opposite sides of the chamber, the walls of the wells constricting towards the chamber so that communication was through narrow slits in order to realize maximum current density on the specimen. The electrodes were connected to an ordinary inductorium, as source of stimuli, by leads passing through a light-tight brass container for holding the lucite assembly, which could be attached to the window of a brass housing of an RCA 1P21 photomultiplier tube. The signal from the photo tube was amplified and fed simultaneously into an Esterline-Angus recorder and a Du Mont type 340 single beam oscillograph.

RESULTS

In most instances, an unpredictable number of repeated stimuli were needed in order to elicit a luminescent response, and the response itself was largely unpredictable with respect to complexity, intensity, and duration. With the method employed, identical successive stimuli could not be given, but oscillograph records of the stimuli (taken separately) indi-

cated a reasonable uniformity. Most likely, therefore, the great variability in response is attributable to unknown physiological factors in the mechanism of excitation.

In only one of a large number of tests did a response occur on the first of a series of consecutive stimulations, consisting of a quick make and break at intervals of approxi-

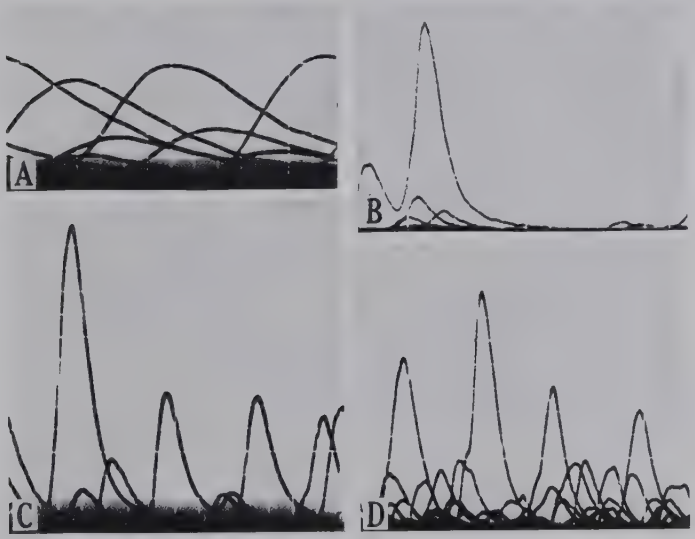

Fig. 1 Luminescent response to single make-break shocks delivered in a sequence at approximately one per second (A and C), and two per second (B and D), with a continuously sweeping oscillograph beam at a frequency of 15 per second in (A), and two per second in (B), (C), and (D). The response first occurred on the 14th consecutive stimulus in (A), on the tenth in (B), principally on the 24th, after very slight responses on the 18th, 19th and 20th in (C), and on the 30th and 40th in (D).

mately one second. A response rarely occurred on the second or third such stimulation; more often it was on about the 10th, and sometimes not until the 40th. Figure 1 (A-D) illustrates the nature of representative responses. Figure 2 shows the 4 most clearly discernible flashes of figure 1 (A) plotted from the oscillograph tracings, arbitrarily taking the same

zero time as that of beginning of response. This time could not be very accurately determined from the record. In figure 2, as plotted however, the time to reach one-half maximum intensity varied from 11 to 12.5 milliseconds, being progressively longer the higher the maximum, and the time for one-half decay varied in a similar manner from 20 to 23.5 milliseconds. The form of the flash in *Polycirrus* resembles that of *Mnemiopsis* (Chang, '54), but these rates of rise and fall of light intensity, in terms of the time to reach half the maximum intensity and to fall to one-half this intensity, respectively, are nearly three times faster at the temperature

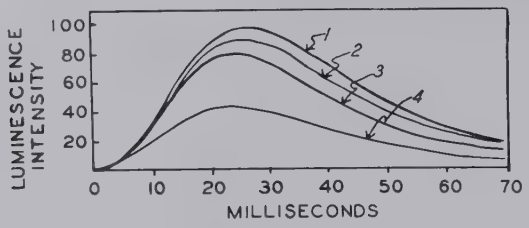

Fig. 2 Four flashes plotted from the oscillograph tracings shown in figure 1 (A), arbitrarily taking the beginning of the response as zero time in each case.

(24–26°C) involved. The rate of decay was exponential as in *Mnemiopsis,* and the same for each of these flashes, as shown by the straight lines with essentially parallel slopes in figure 3, relating the logarithm of decreasing luminescence intensity to time.

In these experiments there was no way to tell from how many, or from what sized, photogenic areas the individual flashes arose, though a solution to this problem could be undertaken with appropriately dissected portions of the tentacles. If the visually observed slow flash, occurring spontaneously or resulting from mechanical stimulation, involves a series of short flashes such as those of figure 1, a fairly large number must take place in the locally luminous area; otherwise, evidence of flicker should become apparent, whereas

none has been reported, nor was any noticed in routine observations in the present study. It would seem more probable that the ordinarily observed response resembles the response to faradic stimulation, as described below.

The results of a series of faradic stimulations of approximately one second duration each, are illustrated in figure 4. Here again, the number of luminescent areas involved is un-

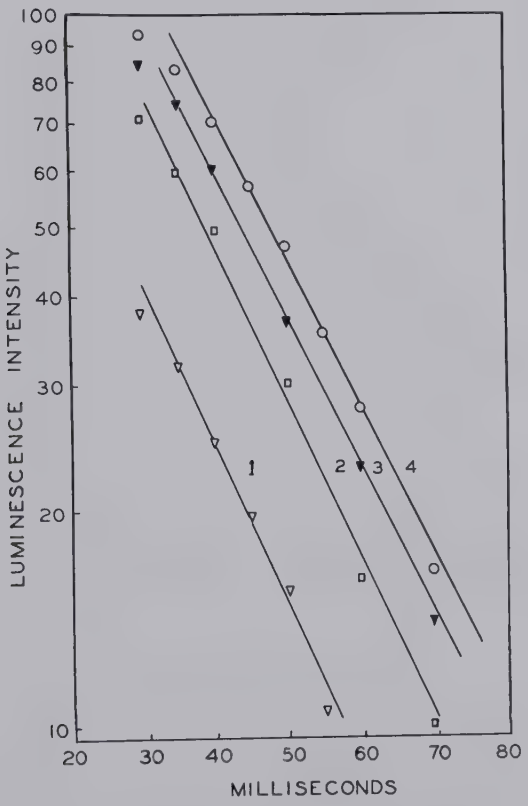

Fig. 3 Rate of decay of luminescence from the maximum, plotted as relative intensity on the logarithmic scale of the ordinate against milliseconds on the abscissa, from the data of figure 2.

fortunately unknown, and it is difficult to tell the precise extent to which the total response consists of summated and fused short flashes. Evidence that short flashes are involved, at least in part, however, is apparent in the wavy character

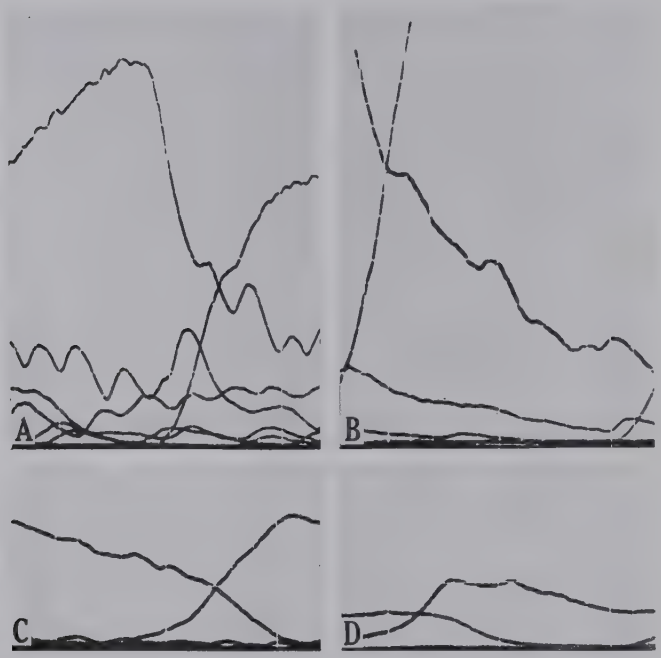

Fig. 4 Responses to 4 consecutive faradic stimulations. A few minutes elapsed between (A) and (B), but (B), (C), and (D) were in close sequence. Amplification of luminescence intensity in (A) and (B) was three times that in (C) and (D). Continuously sweeping oscillograph beam, at a frequency of two per second. Duration of stimulus was approximately 1 sec. for (B), (C), and (D), and several seconds for (A).

of the decay curve in figure 1 A. For the total response, the time to reach half-maximum intensity, as nearly as could be determined from the records, was 132, 166, and 158 milliseconds for figures 1 (A), (C), and (D), respectively, or about

10 times that required in a single, short flash (figs. 1 and 2). Moreover, the maximum tended to be prolonged and the decay slower than exponential.

Some experiments were carried out with respect to the influence of di-isopropylfluorophosphonate (DFP) on the luminescence of this organism, but the oscillograph records were made useless through an error in sweep frequency. The Esterline-Angus records of responses to faradic stimulation of approximately one second's duration indicated that DFP, in a concentration of 0.001 M that reversibly reduces bacterial luminescence (Johnson and Plough, '58), did not abolish the response but made it flatter and more drawn out, with something of an afterglow. Addition of 0.008 M atropin did not counteract this effect. After washing the specimen in several changes of sea water, and allowing repeated 5- to 10-minute rest periods between further faradic stimulations, the sharper form of the flash, without afterglow, again appeared on the Esterline-Angus records, though the maximum intensity which had been generally lower in the DFP solutions, was not regained.

SUMMARY

The luminescent response of *Polycirrus sp.* to repeated inductorium shocks consists of short flashes, of the order of a tenth of a second in duration, with times of slightly over 10 milliseconds to reach half maximum intensity, and 20 to 24 milliseconds for one half decay, as registered on a photomultiplier with oscillograph recorder, at 24 to 26°C. The response rarely occurred on the first stimulus and usually 10 or 12 make-break stimuli at one-second intervals were required, though occasionally as many as forty. The rate of decay from maximum intensity was exponential.

Faradic stimulation elicited a more continuous response, reaching half maximum intensity and one half decay, respectively, in about 10 times the lengths of time required to reach the corresponding points in the short flash. The maximum was broader, and the rate of decay slower than expo-

nential. In some instances evidence of short flashes superimposed on the more gradual course of light intensity was apparent.

In a concentration of 0.001 M, DFP did not abolish the response to short, faradic stimulation, but flattened the course of light intensity versus time, and resulted in an afterglow, according to Esterline-Angus recordings. The DFP effects were not counteracted by 0.008 M atropin, but the more characteristic type of response gradually returned after washing with several changes of sea water.

ACKNOWLEDGMENTS

The authors are pleased to acknowledge their indebtedness to Dr. Robert Hiatt, Dr. A. H. Banner and other members of the staff of the Hawaii Marine Laboratory for providing laboratory facilities and for helpful cooperation in various ways, and to Dr. Olga Hartman, for kindly identifying the organisms from preserved specimens.

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ZOOLOGY

A new species of Haloptilus *(Copepoda: Calanoida) from equatorial and subtropical waters of the east-central Pacific Ocean*

George D. Grice

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ZOOLOGY—*A new species of* Haloptilus *(Copepoda: Calanoida) from equatorial and subtropical waters of the east-central Pacific Ocean*[1]. GEORGE D. GRICE,[2] Woods Hole Oceanographic Institution, Woods Hole, Mass. (Communicated by Paul L. Illg.)

(Received April 3, 1959)

The new species of *Haloptilus* described below was found while examining a series of plankton samples which had been collected by the U. S. Fish and Wildlife Service as part of their oceanographical and marine biological studies in the Pacific Ocean.

Haloptilus austini, n. sp.

Figs. 1–18

Localities and materials.—Latitude 28°00′N., longitude 159°03′W. (U. S. Fish and Wildlife Service *Hugh M. Smith* Cruise 27, station 67, February 19, 1955, 100–0 m depth of tow, 1 female); latitude 00°11′S., longitude 119°58′W. (*Hugh M. Smith* Cruise 31, station 94-2, November 7, 1955, 146–72 m depth of tow, 2 females). Physical oceanographic and other data for Cruise 27 are summarized by McGary and Stroup (1958) and that for Cruise 31 by King, Austin, and Doty (1957).

Types.—All three specimens have been deposited in the U. S. National Museum. A female from Cruise 31 was selected as the holotype (U.S.N.M. no. 102742). Paratype numbers are as follows: U.S.N.M. no. 102744 (1 female, Cruise 31) and U.S.N.M. no. 102743 (1 female, Cruise 27).

Description.—Female (Figs. 1–18). The cephalothorax is much longer than the abdomen, the ratio of these two body parts being approximately 8 to 1 (Fig. 1). The head is rounded and considerably produced anteriorly (Figs. 1 and 2). A convex protrusion is present on each side at a point adjacent to the origin of the second antennae. The rostral filaments (Figs. 2 and 3) arise from two small elevations which are situated a short distance in front of the origin of the first antennae.

The abdomen (Figs. 4, 5, and 6) consists of 4 segments. The genital segment is longer than the combined lengths of the succeeding 3 segments.

The first antennae of all three specimens are broken off at segment 22. When held against the body, segment 20 reaches to approximately the end of the caudal furcae. The endopod of the second antennae (Fig. 7) is a little less than twice the length of the exopod. The exopod consists of 7 segments. Segment 1 has 2 setae. Segments 2 through 6 are furnished with a single seta. There are 4 setae on segment 7. The first segment of the endopod has 2 setae situated just beyond the mid-point of this segment. The external lobe of the second endopodal segment has 6 large and 1 minute seta. The internal lobe has 8 setae, 4 of which are notably small.

The exopod of the mandible (Fig. 8) is a little more than one-half the length of the endopod. The former apparently consists of 5 segments, the first 4 of which are furnished with a seta. The terminal segment has 2 setae. Segment 1 of the endopod has 2 setae distally, and segment 2 is provided with 8 terminal setae. The gnathal lobe of the mandible is shown in Fig. 9.

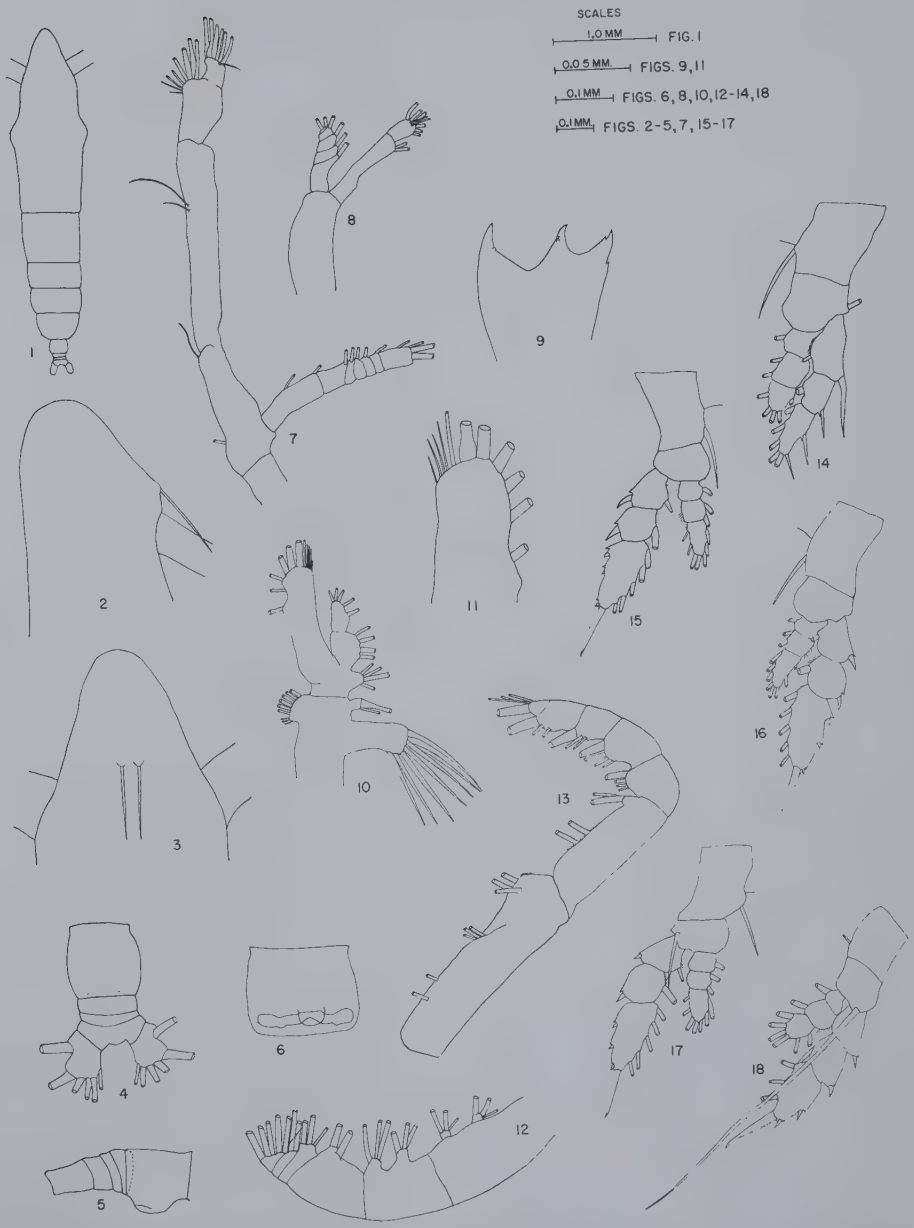
The first maxilla is shown in Fig. 10. The exopod is elongate and furnished with 11 setae. Four of the setae on the distal margin are quite small and slender (Fig. 11). The endopod carries 5 setae, and the second basal segment bears 4 setae. Inner lobes 1, 2 and 3 bear 7, 2 and 4 setae, respectively. The external lobe has 6 large and 3 small setae.

The second maxilla (Fig. 12) has 6 lobes. Lobes 1 through 4 and lobe 6 have 3 setae. Lobe 5 has 2 setae. The distal part of this appendage is furnished with 7 setae.

The maxilliped (Fig. 13) consists of 2 basal and 5 endopodal segments. The first basal segment has 2 setae near the proximal end, 3 setae near the center, and 3 setae near the distal end. The second basal segment is furnished with 2 setae near the center and 2 setae on the distolateral corner. Endopodal segments 1 and 2 have 4 setae and segments 3 and 4 have 3 setae. The fifth segment is furnished with 1 seta and 3 bristles.

The first to fourth pairs of swimming feet are

[1] Contribution No. 116 Hawaii Marine Laboratory, University of Hawaii.
[2] Fellow of the John Simon Guggenheim Memorial Foundation, 1958–1959.



FIGS. 1–18.—*Hatoptilus austini*, n. sp., female: 1, Dorsal; 2, forehead, lateral view; 3, forehead, ventral view; 4, abdomen, dorsal view; 5, abdomen, lateral view; 6, genital segment, ventral view; 7, second antenna; 8, mandibular palpus; 9, gnathal lobe of mandible; 10, first maxilla; 11, terminal part of exopod of first maxilla; 12, second maxilla; 13, maxilliped; 14, first foot; 15, second foot; 16, third foot; 17, fourth foot; 18, fifth foot. Fig. 11 drawn from paratype. All other figures drawn from holotype.

shown in Figs. 14 through 17. The first pair of feet is smaller than the succeeding 3 pairs. There is 1 seta on the internal margin of basipodal segment 1 and 1 seta on the external margin of basipodal segment 2. Both exopod and endopod consist of 3 segments. Segments 1 and 2 of the exopod have 1 long external spine and 1 internal seta. Segment 3 has 2 external spines and 4 internal and 1 terminal seta. Endopodal segment 1 has 1, segment 2 has 2, and segment 3 has 5 setae.

The second, third, and fourth pairs of feet are similar. Basipodal segment 1 has an internal seta. Basipodal segment 2 of the second and third feet is naked. This segment of the fourth feet is furnished with an external seta. Segments 1 and 2 of the exopod have a small external spine and a single internal seta. The third exopodal segment has a terminal, finely serrate spine. There are 3 small external spines and 5 internal setae on this segment. In the second and fourth pairs of feet, endopodal segment 1 has 1 seta, segment 2 has 2 setae, and segment 3 has 7 setae. In the third pair of feet the numbers of setae on these respective segments of the endopod are 1, 2, and 8.

The fifth pair (Fig. 18) of feet is smaller than the preceding 3 pairs. Basipodal segment 1 has 1 internal seta. Basipodal segment 2 is furnished with 1 seta which exceeds the tip of the terminal exopodal spine. Exopodal segment 1 has 1 external spine, segment 2 has 1 external and 1 internal spine, and segment 3 has 2 external and 1 terminal spine. Segment 3 is also furnished with 3 internal setae. Endopodal segments 1, 2, and 3 are provided with 1, 1, and 6 setae, respectively.

Total length of the three specimens is as follows: 3.33 mm (holotype), 3.16 mm (paratype, Cruise 31) and 3.06 mm (paratype, Cruise 27).

No male has been found.

Remarks.—This species resembles *H. chierchiae* (Giesbrecht) but may readily be distinguished from it by the shape of the head and the structure of the first maxillae and fifth pair of feet. The head of *H. austini* is considerably more produced anteriorly. In regard to the first maxilla of *H. austini*, the second basal segment has 4 setae, the exopod has 11 setae, and the endopod has 5 setae. The corresponding parts of the first maxilla of *H. chierchiae*, as figured by Giesbrecht (1892) and Sars (1924), have 5 setae, 8 setae, and 7 setae. The seta on the second basal segment of the fifth pair of legs of *H. austini* exceeds the tip of the terminal exopodal spine. In *H. chierchiae* this seta, as figured by Sars (1924), does not reach the distal end of the second exopodal segment. This new copepod is named in honor of Thomas S. Austin, oceanographer, Honolulu Biological Laboratory, U. S. Fish and Wildlife Service.

Acknowledgments.—The Honolulu Biological Laboratory, U. S. Fish and Wildlife Service, provided laboratory space during the course of the investigation. Dr. W. Vervoort has kindly read the manuscript.

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They will tell you to try to prove you are right; I tell you to try to prove you are wrong.—LOUIS PASTEUR.

The Hawaiian Species of *Conus* (Mollusca: Gastropoda)

ALAN J. KOHN

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October, 1959

The Hawaiian Species of *Conus* (Mollusca: Gastropoda)[1]

ALAN J. KOHN[2]

IN THE COURSE OF a comparative ecological study of gastropod mollusks of the genus *Conus* in Hawaii (Kohn, 1959), some 2,400 specimens of 25 species were examined. Uncertainty of the correct names to be applied to some of these species prompted the taxonomic study reported here. Many workers have contributed to the systematics of the genus *Conus;* nevertheless, both nomenclatorial and biological questions have persisted concerning the correct names of a number of species that occur in the Hawaiian archipelago, here considered to extend from Kure (Ocean) Island (28.25° N., 178.26° W.) to the island of Hawaii (20.00° N., 155.30° W.).

FAUNAL AFFINITY

As is characteristic of the marine fauna of the Hawaiian Islands, the affinities of *Conus* are with the Indo-Pacific center of distribution. The Hawaiian Islands mark the northeastern limit of most of the species that occur there. Eastern Pacific species of *Conus* are entirely absent from the Hawaiian fauna.

Most of the species present in Hawaii range widely throughout the central and western Pacific Ocean, Indian Ocean, and Red Sea. The chief mode of distribution is the pelagic veliger larval stage. Drifting while attached to floating material may be a secondary mechanism. Despite the extensive distribution of most of the species occurring in Hawaii, the geographic position of the archipelago and the prevailing westerly surface currents are factors which could plausibly effect the isolation necessary for geographic speciation.

Of the 33 species of *Conus* considered in this paper to be valid constituents of the Hawaiian fauna, about 20 occur in shallow water on marine benches and coral reefs and in bays. Of these, only one species, *C. abbreviatus* Reeve, is considered to be endemic to the Hawaiian archipelago. Less is known of the species more characteristic of deeper water habitats. Some, known at present only from dredgings about the Hawaiian Islands, may in the future prove to occur elsewhere as well, when adequate sampling methods are extended to other parts of the Indo-West Pacific region.

ECOLOGY

Since the ecology of *Conus* has been discussed in detail elsewhere (Kohn, 1959), ecological data are restricted to notes in this report.

It is a pleasure to acknowledge the constant stimulation and willing assistance of Karl W. Greene, director, Children's Museum of Honolulu, and Edwin H. Bryan, Jr., curator of collections, Bernice P. Bishop Museum, Honolulu. The collections and libraries of the following institutions were also visited, and gratitude is expressed to the persons in charge: U. S. National Museum (H. A. Rehder, J. P. E. Morrison), Academy of Natural Sciences of Philadelphia (R. T. Abbott), Museum of Comparative Zoology, Harvard University (W. J. Clench, R. D. Turner), and Bernice P. Bishop Museum (Y. Kondo). In addition, specimens were loaned to the writer for study by C. A. Allen, Mrs. Jean Bromley,

[1] Contribution No. 117, Hawaii Marine Laboratory. Manuscript received July 30, 1957.

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Mrs. A. M. Harrison, W. C. Ross, and C. S. Weaver. Valuable assistance rendered by Charles E. Cutress in preparation of the color photographs is gratefully acknowledged. Most of the work was carried out at the Osborn Zoological Laboratory, Yale University, during tenure of a fellowship from the National Science Foundation.

BIBLIOGRAPHICAL NOTES

An excellent bibliographical account and collation of the major works in which species of *Conus* were described is given by Hanna and Strong (1949). Except where otherwise noted, the collations cited therein are followed in the present paper.

Catalogue of the Portland Museum. 1786. This catalogue was published anonymously, but its authorship is usually attributed to George Humphrey (Dall, 1921). The names of new species are attributed to Daniel Solander in the volume, and the same usage is followed in the present paper. A valuable discussion of this catalogue is given by Wilkins (1955), who also presents cogent reasons for attributing the names to Humphrey.

J. G. Bruguière. *Encyclopédie Méthodique. Histoire Naturelle des Vers.* 1792. Many previously undescribed species of *Conus* were named and carefully described in this work. However, the authorship to be attributed to these names has been a matter of dispute almost since the volume appeared. In the volume, Bruguière attributes the names and Latin diagnoses of species to C. H. Hwass (p. 598). Bruguière states that he himself wrote the descriptions and the "additional" synonymy (see Clench, 1942: 3). New specific names are published in the volume as, e.g. "*Conus catus* Hwass."

However, many subsequent writers (Lamarck, 1810; Dillwyn, 1817; Kiener, 1845–1850; Wood, 1856; Sowerby, 1857–1858; Schaufuss, 1869; Iredale, 1929; Tomlin, 1937; Cotton, 1945; Hanna and Strong, 1949; Hirase, 1954; and Kira, 1955) have cited such species as, e.g. "*Conus catus* Bruguière." Other writers (Blainville, 1818; Reeve, 1843–1844; Adams and Adams, 1858; Weinkauff, 1874; Smith, 1879; Tryon, 1884; Fischer, 1887; von Martens and Thiele, 1903; Tinker, 1952; and Morris, 1952) have cited the names as they appear in Bruguière (1792). A third group of writers (Dautzenberg, 1937; Clench, 1942; Mermod, 1947; and Dodge, 1953) has cited such names as, e.g., "*Conus catus* Hwass *in* Bruguière."

Application of the *Règles* of the International Commission on Zoological Nomenclature (ICZN), and later provisions and clarifications of the *Règles*, does not lead to an unequivocal solution to this problem. In the decisions of the ICZN meeting in Paris in 1948, it was recommended (Bull. Zool. Nomencl. 4: 565–566, 1950) that "where in a book or paper written by one author (say author 'A') it is clearly stated that the description of one or more specified taxonomic units there named has been prepared exclusively by some other author (say author 'C'), the name or names in question are to be attributed to author 'C', not to author 'A'. The name of the taxonomic unit so described and named is to be cited by later authors as having been published by 'C in A'."

It is apparent from the remarks of Bruguière (1792: 598; see also Clench, 1942: 3) that the descriptions of the species were not prepared exclusively by Hwass, although the names and brief Latin diagnoses were. It is, however, the present author's opinion that Hwass's contribution is sufficient to justify attributing authorship of the names to him. This view is strengthened by the more recent further clarification of Article 21 (Copenhagen Decisions, 1953: 58–59), which states that "the rule set out on pages 565–566 of vol. 4 of the BULLETIN should be qualified in such a way as to make it clear that it applies only where the book or paper concerned contains a clear indication that not only the name in question was proposed by some author other than that by whom the book or paper was written but also that the indication, defini-

tion, or description on which, under Article 25, the availability of that name depends was written not by the author of the book or paper concerned but by the author to whom the name is there attributed."

For these reasons, the species of *Conus* referred to as, e.g. "*Conus catus* Hwass" in Bruguière (1792) are herein cited as, e.g. "*Conus catus* Hwass *in* Bruguière."

Museum Calonnianum. 1797. The names introduced in this publication were rejected in Opinion 51 of the ICZN (Smithsonian Publ. 2060, 1912: 116), but this decision has not been universally accepted. Of the names listed in the Museum Calonnianum, only three, all of which are synonyms, are pertinent to this paper. For the sake of completeness, they are listed in brackets in the synonymies. Authorship of the Museum Calonnianum is attributed to George Humphrey, following general acceptance. The problem is discussed in detail by Iredale (1937).

Museum Boltenianum. 1798. The names in this volume were accepted as nomenclatorially available in Opinion 96 of the ICZN (Smithsonian Misc. Coll., 73(4): 16–18, 1926), and their authorship was attributed to P. F. Röding in Direction 48 of the ICZN (Opinions and Declarations Rendered by the ICZN, 1: 255–264, 1956).

L. W. Dillwyn. *A Descriptive Catalogue of Recent Shells*. 1817. A number of species of *Conus* described by Chemnitz (1788, 1795) are listed in Dillwyn's catalogue. Since the specific names in Chemnitz (1788, 1795) have been rejected by Opinion 184 of the ICZN (Opinions and Declarations Rendered by the ICZN, 3: 27–35), these names became nomenclatorially available upon publication by Dillwyn (1817). (See also Bull. Zool. Nomencl., 4: 259–260, 1950.)

L. C. Kiener. *Spécies Général et Iconographie des Coquilles Vivantes*. 1845–1850. The names of species described in this work appear both on the plates and in the text. Hanna and Strong (1949) reproduce the summary of the collation of Sherborn and Woodward (1901: 218) which gives 1846 as the year of publication of the plates. This date, however, is erroneous, being presumably a typographical error. The correct date is 1845 as given in the body of the paper (Sherborn and Woodward, 1901: 217). Therefore, the names in Kiener's work should date from 1845 rather than from the dates on which they appeared in the text.[3]

Tomlin (1937) has given the most complete catalogue of the genus *Conus*. Some 2,700 names are listed, including both extant and fossil species. Earlier catalogues of Recent species are given by Reeve (1843–1849), Kiener (1845–1850), Sowerby (1857–1858), and Tryon (1884).

Earlier published lists of the species of *Conus* in Hawaii are those of Garrett (1878), Edmondson (1933, 1946), Tinker (1952, 1958), and Greene (1953). Extensive unpublished lists compiled by W. A. Bryan in 1919, and by E. H. Bryan, Jr. in 1956, have been made available to the writer by E. H. Bryan, Jr.

SYNONYMY

The synonymies consist of the first known publication of all known different names, authors, and combinations which have been applied to the species, listed chronologically. Subsequent references to the same name are not given, with the exception of errors and emendations, in order to conserve space. It is perhaps unfortunate that some of the references are to distributional lists and museum catalogues, which in many cases lack taxonomic information. These are included primarily because specific names first published in some of the museum catalogues have been recognized as available by the ICZN. Furthermore, in addition to their historical importance, such lists and catalogues are in some cases the source of errors which have been perpetuated in the subsequent literature.

Many specific names of *Conus* were introduced by authors who did not consistently use the binominal system. These names are

[3] The author is grateful to Dr. Harald A. Rehder for having pointed out this discrepancy.

thus invalid (see Opinions and Declarations Rendered by the ICZN, 3: 27–35; 5: 265–279) and have not been included in the synonymies. Among the post-Linnean authors responsible for such names are Martini (1773), Chemnitz (1788, 1795), Meuschen (1778, 1787), and Martyn (1784–1792).

In cases of generic changes by subsequent authors, the name of the author of the species has been placed in parentheses throughout, whether or not this was done by the author of the generic change.

Described varieties of listed valid species are not included in synonymies. However, if the listed valid species itself has been described as a variety of another species, that entry is included in the synonymy.

In cases of published erroneous identification of specimens, the notation "(error)" follows the entry.

Genus CONUS Linné

Shell obconical, turbinate; whorls enrolled upon themselves, attenuated anteriorly. Spire usually short, smooth or coronate. Aperture elongate, narrow, effuse at the base, without teeth; outer lip smooth, sharp, with a sutural sinus.

Conus abbreviatus Reeve

Fig. 33 in Plate 2

Conus abbreviatus Reeve, 1843, Conch. Icon., 1: pl. 16, sp. 86.

Conus abbreviatus Sowerby, 1857, Thes. Conchyl., 3: 10 (as "*C. abbreviatus* Nuttall MS., Reeve C.I." on pl. 4, fig. 84).

Conus coronatus Dillwyn var. *abbreviatus*. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 250.

Conus miliaris Hwass var. *abbreviatus*. Tryon, 1884, Man. Conch., 1: 22, pl. 5, fig. 89.

Stephanoconus abbreviatus (Reeve). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 4.

DESCRIPTION: Shell small but sturdy. Body whorl striate, the striae as raised ridges near the base, impressed and widely spaced elsewhere. Aperture fairly narrow, flaring somewhat towards the anterior, or basal end. Base attenuated. Shoulder coronate; spire depressed, coronate, striate. Color bluish gray, with pale flesh-colored transverse bands in the middle of the body whorl and at the shoulder; with rows of rather distantly spaced small brown dots encircling the body whorl. Aperture purplish brown within, with a light median band. Periostracum thin, yellow, translucent. In life, foot pale brown; siphon pale brown, tinged with pink.

LENGTH: To 60 mm., but usually smaller.

TYPE LOCALITY: Oahu.

REMARKS: It is believed that this species is endemic to the Hawaiian archipelago. It is known from Midway Island and all of the main islands, where it is usually rather common on marine benches. Larger specimens are found on sandy substrata of coral reef platforms.

Conus miliaris Hwass and *C. coronatus* Gmelin, neither of which occurs in Hawaii, are the most closely related species. *C. abbreviatus* may be distinguished from both by the regular arrangement and small size of the brown dots, by the characteristic bluish-gray ground color, and by the absence of irregular longitudinal white flecks (as in *C. miliaris*) or brown blotches (as in *C. coronatus*).

Pleistocene fossils of *C. abbreviatus* are known from Oahu (Ostergaard, 1928), Maui, and Molokai (Ostergaard, 1939).

Conus acutangulus Lamarck

Fig. 37 in Plate 2

Conus acutangulus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 286.

Leptoconus acutangulus. Adams and Adams, 1853, Gen. Rec. Moll., 1: 251.

Conus acutangulatus Sowerby, 1857, Thes. Conchyl., 3: 11.

(?) *Conus crebrisulcus* Sowerby, 1857, Thes. Conchyl., 3: 21, pl. 14, fig. 321.

Conus turriculatus Sowerby, 1866, Thes. Conchyl., 3: 328, pl. 27, figs. 643, 644.
Conus gemmulatus Sowerby, 1870, Proc. Zool. Soc. Lond., 1870: 257, pl. 22, fig. 8.
Conus acutangulus Bruguière. Paetel, 1883, Catal. Conch.-Samml. Paetel, p. 50.
Conus acutangulus Hwass. Tryon, 1884, Man. Conch., 6: 76.
Conus acutanculus Friedberg, 1911, Rozprawyi Wiadomości Muzeum Imienia Dzieduszyckich (Moll. Mioc. Poloniae), 14: 47.
Conus eugrammatus Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 85.
Conasprella acutangulus (Lamarck). Cotton, 1945, Rec. South Austral. Mus., 8: 272.
Conus eugrammatus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.
Asprella acutangulus (Lamarck). Kuroda, 1956, Venus: Jap. Jour. Mal., 19: 88.

DESCRIPTION: Shell small, rather thin. Body whorl elongate, bearing rather distantly and irregularly spaced incised spiral lines marked by small punctures. Aperture narrow, outer lip protracted. Shoulder angular, ridged; spire elevated, turreted, concave, striate, comprising at least one third of the total shell length; apex sharp. Early whorls smooth, succeeding whorls with slender protracting curved axial riblets which fuse to form strong nodules at the shoulder, the nodules becoming less conspicuous on the latest whorls. Color of body whorl white to pale buff, marked with interrupted broad brown spiral bands either side of the center. Rows of brown dots between the striae mark the light area between the brown bands. Spire marked by distantly spaced rather regular broad brown spots. Periostracum grayish white, bearing lamellae on the fine riblets of the spire.

LENGTH: 30 mm.

TYPE LOCALITY: "Mers des grandes Indes."

REMARKS: Specimens of *C. acutangulus* have been collected in Hawaii by dredging in comparative shallow water and to a depth of 200 fathoms.

Conus bullatus Linné

Fig. 1

Conus bullatus Linné, 1758, Syst. Nat., ed. 10, p. 717.

PLATE 1

References are given to the shells figured. The dimensions given are shell length × maximum diameter.

FIG. 1. *Conus distans* Hwass *in* Bruguière. 75 × 43 mm. Off Rabbit (Manana) Island, off Oahu. USNM coll., No. 484738.

FIG. 2. *Conus textile* Linné. 80 × 44 mm. Waikiki, Oahu. C. E. Cutress coll.

FIG. 3. *Conus pennaceus* Born. 64 × 35 mm. Keaukaha, Hilo, Hawaii. USNM coll., No. 338584.

FIG. 4. *Conus quercinus* Solander. 80 × 49 mm. Honolulu Harbor Channel, Oahu. USNM coll., No. 338584.

FIG. 5. *Conus striatus* Linné. 107 × 53 mm. Waikiki, Oahu. C. E. Cutress coll.

FIG. 6. *Conus miles* Linné. 67 × 39 mm. Waikiki, Oahu. C. E. Cutress coll.

FIG. 7. *Conus imperialis* Linné. 69 × 36 mm. Lahaina, Maui. USNM coll., No. 484735.

FIG. 8. *Conus spiceri* Bartsch & Rehder. 113 × 62 mm. Midway Island. USNM coll., No. 523700.

FIG. 9. *Conus marmoreus* Linné. 96 × 54 mm. Honolulu Harbor entrance, Oahu, 5–8 fathoms. USNM coll., No. 338163.

FIG. 10. *Conus leopardus* (Röding). 143 × 86 mm. Waimea Bay, Oahu. C. E. Cutress coll.

FIG. 11. *Conus vexillum* Gmelin. 88 × 54 mm. Kahala, Oahu. USNM coll., No. 338510.

FIG. 12. *Conus pulicarius* Hwass *in* Bruguière. 48 × 27 mm. Honolulu, Oahu. USNM coll., No. 338195.

FIG. 13. *Conus smirna* Bartsch & Rehder. Holotype. 61 × 23 mm. off Lanai, 257–312 fathoms. USNM coll., No. 173226.

FIG. 14. *Conus vitulinus* Hwass *in* Bruguière. 56 × 31 mm. Keokea, Hawaii. USNM coll., No. 338549.

FIG. 15. *Conus litoglyphus* Hwass *in* Bruguière. 41 × 19 mm. Honolulu Harbor entrance, Oahu, 5–8 fathoms. USNM coll., No. 338538.

FIG. 16. *Conus moreleti* Crosse. 46 × 23 mm. Kailua, Oahu, 12–15 feet. USNM coll., No. 484249.

FIG. 17. *Conus lividus* Hwass *in* Bruguière. 39 × 23 mm. Honokowai, Maui. USNM coll., No. 338531.

FIG. 18. *Conus flavidus* Lamarck. 42 × 25 mm. Honokowai, Maui. USNM coll., No. 338522.

FIG. 19. *Conus nussatella* Linné. 53 × 17 mm. Kuhio Bay, Hilo, Hawaii. USNM coll., No. 338577.

Conus nubecula Gmelin, 1791, Syst. Nat., ed. 13, p. 3396.
Cucullus nubecula (Gmelin). Röding, 1798, Mus. Boltenianum, p. 46.
Cucullus parvus Röding, 1798, Mus. Boltenianum, p. 46.
Cucullus laganum Röding, 1798, Mus. Boltenianum, p. 51.
Conus bullatus Lamarck. Sowerby, 1833, Conch. Illus., p. 2, pt. 29, fig. 23.
Textilia bullatus. Swainson, 1840, Treat. Mal., p. 312.
Leptoconus bullatus (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 253.
Textilia bullata (Linné). Cotton, 1945, Rec. South Austral. Mus., 8: 261.

DESCRIPTION: Shell rather thick but not heavy, ovate-oblong, the maximum diameter not at the shoulder but about one third of the distance from shoulder to base. Body whorl glossy, with impressed, rather widely spaced transverse striae basally. Shoulder rounded, smooth; spire obsoletely striate, canaliculate. Ground color white or pale pink, clouded with orange brown subtrigonal markings often fused to form three broad, rather poorly defined transverse bands, separated by areas of sparser, irregularly placed similar markings. Spire marked irregularly with orange brown and pink or pinkish white. Interior of aperture pinkish orange. Periostracum thin.

LENGTH: The most recently collected specimen from Hawaii (see below) measures 62 × 29 mm.

TYPE LOCALITY: None.

REMARKS: Very few specimens of *Conus bullatus* are known from the Hawaiian Islands. A single shell in excellent condition was dredged off Nanakuli, Oahu, but whether or not it was alive is not known (D. Thaanum, *in litt.*). In November, 1957, a living specimen (Fig. 1) was collected half-buried in sand at a depth of 100 feet off Diamond Head, Oahu (C. S. Weaver, *in litt.*). At least two other specimens are believed to have been collected in Hawaii, but it has not been possible to verify the reports. In addition, a number of dead shells have been collected (K. W. Greene, *in litt.*; L. Brand, verbal communication).

Conus capitaneus Linné

Fig. 2

Conus capitaneus Linné, 1758, Syst. Nat., ed. 10, p. 713.

PLATE 2

References are given to the shells figured. The dimensions given are shell length × maximum diameter.

FIG. 20. *Conus ebraeus* Linné. 39 × 23 mm. Hilo. Hawaii. USNM coll., No. 338209.

FIG. 21. *Conus chaldaeus* (Röding). 29 × 18 mm. Hilo, Hawaii. USNM coll., No. 338477.

FIG. 22. *Conus tessulatus* Born. 42 × 25 mm. "Sandwich Is." USNM coll., No. 5038. A faded specimen.

FIG. 23. *Conus quercinus* Solander. 33 × 16 mm. Off Kaanapali, Maui, 4–12 fathoms. USNM coll., No. 338187. Juvenile specimen, showing the characteristic high spire.

FIGS. 24–28. *Conus suturatus* Reeve, showing changes in color pattern with increase in size. FIG. 24. 23 × 11 mm. Off Launiupoko Camp, Maui, 4–12 fathoms. USNM coll., No. 338546. FIG. 25. 25 × 13 mm. Off Mt. Lihau, Maui, 4–12 fathoms. USNM coll., No. 338547. FIG. 26. 32 × 17 mm. USNM coll., No. 338546. FIG. 27. 37 × 21 mm. Honolulu Harbor entrance, Oahu, 5–8 fathoms. USNM coll., No. 338541. FIG. 28. 48 × 27 mm. North Island, Pearl and Hermes Reef. Mrs. J. Bromley coll., No. 3363.

FIG. 29. *Conus catus* Hwass *in* Bruguière. 29 × 18 mm. Honokowai, Maui. USNM coll., No. 338561.

FIG. 30. *Conus rattus* Hwass *in* Bruguière. 30 × 17 mm. Honolulu, Oahu. USNM coll., No. 338516.

FIG. 31. *Conus pertusus* Hwass *in* Bruguière. 30 × 15 mm. Locality unknown. USNM coll., No. 18522.

FIG. 32. *Conus retifer* Menke. Midway Island. USNM coll., No. 524591. A faded specimen.

FIG. 33. *Conus abbreviatus* Reeve. 26 × 17 mm. Honokowai, Maui. USNM coll., No. 338488.

FIG. 34. *Conus circumactis* Iredale. 22 × 11 mm. Off Lanai, 179–253 fathoms. (Holotype of *Conus hammatus* Bartsch and Rehder). USNM coll., No. 173225. Juvenile.

FIG. 35. *Conus circumactis* Iredale. 17 × 9 mm. USNM coll. Juvenile.

FIG. 36. *Conus obscurus* Sowerby. 23 × 9 mm. Off Waikiki, Oahu, 20 feet. USNM coll., No. 484740.

FIG. 37. *Conus acutangulus* Lamarck. 24 × 10 mm. Honolulu Harbor entrance, Oahu, 6–8 fathoms. USNM coll., No. 338564.

FIGS. 38–39. *Conus sponsalis* Hwass *in* Bruguière. Kauai. USNM coll. FIG. 38. 15 × 9 mm. FIG. 39. 18 × 11 mm.

FIG. 1. *Conus hullatus* Linné, 62 × 29 mm. Collected off Diamond Head, Oahu, 17 fathoms. Shell in collection of C. S. Weaver. Photographs by the author.

Conus classiarius Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 705, pl. 335, fig. 7.
[*Conus venator* Humphrey, 1797, Mus. Calonnianum, p. 11.]
[*Conus agasus* Humphrey, 1797, Mus. Calonnianum, p. 11.]
Cucullus capitaneus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 43.
Conus classiarius Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 267.
Conus chemnitzii Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 363.
Conus capitaneus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 172.
Leptoconus capitaneus (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.
Conus ceciliae Crosse, 1858, Jour. Conchyl., 7: 381, pl. 14, fig. 5.
Rhizoconus capitaneus (Linné). Frauenfeld, 1869, Verh. Zool.-Bot. Ges. Wien, 19: 863.
Conus chemnitzi Dillwyn. Dautzenberg, 1937, Mem. Mus. Roy. Hist. Nat. Belg., 2(18): 171.
Lithoconus capitaneus (Linné). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 4, fig. 9.

DESCRIPTION: Shell of moderate thickness; body whorl encircled by finely punctate striae on the basal half, the striae more distinct and separated by low ridges basally; aperture rather narrow, the sides parallel. Shoulder angular, smooth; spire rather low, obtuse, striate; apex pointed. Color of body whorl variable, yellow or olive yellow to orange brown or olive brown, encircled by several dark brown dotted lines and two broad white bands, interrupted by dark brown blotches, at the shoulder and centrally on the body whorl. The white bands may also be crossed by closely spaced longitudinal wavy brown

lines. Young individuals may lack the two white bands. Spire tesselated with alternate brown and white blotches, continuing to form band on body whorl at shoulder. Outer lip thin; aperture violet within. Periostracum rather thin but opaque, encircled by raised transverse ridges.

LENGTH: The only two specimens known from the Hawaiian Islands (Fig. 2) measure 31 × 21 mm. and 19.5 × 11.5 mm.

TYPE LOCALITY: Asia.

REMARKS: This species was not known to occur in the Hawaiian area until the collection of a living specimen (Fig. 2, right) by Mrs. A. M. Harrison at a depth of 15–20 feet off Nanakuli, Oahu, in April, 1958. A second, smaller specimen (Fig. 2, left) was collected by Mr. A. M. Harrison at a depth of 35 feet near Kaena Pt., Oahu, on 31 August 1958.

Conus catus Hwass *in* Bruguière

Fig. 29 in Plate 2

Conus catus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 707, pl. 332, figs. 3, 4, 7.
Conus leoninus var. δ Gmelin, 1791, Syst. Nat., ed. 13, p. 3387.
Cucullus nubilus Röding, 1798, Mus. Boltenianum, p. 46.
Conus nubilus (Bolten). Link, 1807, Beschreib. Nat.-Samml. Univ. Rostock, Abt. 3, p. 105.
Conus catus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 285.
Conus discrepans Sowerby, 1833, Conch. Illus., p. 2, pt. 29, fig. 28.
Conus catus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 173.
Leptoconus catus (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 253.
(?) *Conus purus* Pease, 1862, Proc. Zool. Soc. Lond., p. 279.
Chelyconus catus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 241.
Chelyconus catus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 6, fig. 10.

DESCRIPTION: Shell stout, solid, bulbous. Body whorl striate, the striae raised, rounded, usually obsolete near the shoulder, and granular near the base. Aperture rather broad, the sides almost parallel. Shoulder rounded, smooth; spire obtuse, deeply striate. Apex sharp, rose-colored, but often eroded. Color of body whorl and spire brown with irregular white flecks or splotches. Aperture white with brown margin. Periostracum thin, yellow, translucent. In life, foot mottled brown on buff. "Pale cinereous, varied with delicate brown mottlings, which are most conspicuous on the muzzle" (Garrett, 1878).

LENGTH: To 40 mm.

TYPE LOCALITY: Several localities are given with the original description, the first two of which, "Saint-Domingue" and Martinique, are almost certainly in error. The species described as *Conus catus* is restricted to the Indo-West Pacific region although it resembles *Conus ranunculus* Hwass *in* Bruguière, a western Atlantic species.

REMARKS: *Conus catus* is less variable with respect to shell characteristics in Hawaii than in other parts of the Pacific and Indian oceans. It occurs intertidally on benches and rocky shores and subtidally as well. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus chaldaeus (Röding)

Fig. 21 in Plate 2

Conus princeps Linné. Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 134. (error).
Conus princeps var. β. Gmelin, 1791, Syst. Nat., ed. 13, p. 3378.
Conus ebraeus Linné var. E. Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 619, pl. 321, figs. 1, 7, 8.
Cucullus chaldaeus Röding, 1798, Mus. Boltenianum, p. 42.
Conus chaldaeus (Bolten). Link, 1807, Beschreib. Nat.-Samml. Univ. Rostock, Abt. 3, p. 106.

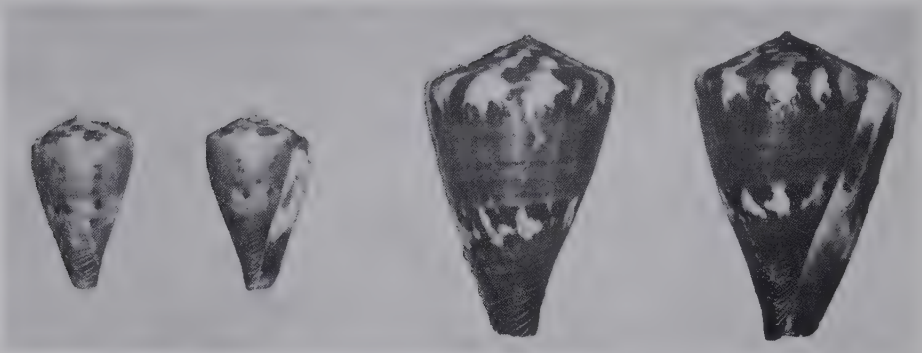

FIG. 2. *Conus capitaneus* Linné. Left, 19.5 × 11.5 mm. Specimen collected by A. M. Harrison near Kaena Pt., Oahu, 6 fathoms. Right, 31 × 21 mm. Specimen collected by Mrs. A. M. Harrison near Nanakuli, Oahu, 3 fathoms. Photographs by the author.

Conus vermiculatus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 34.
Conus ebraeus Linné var. C. Dillwyn, 1817, Descr. Cat. Rec. Shells, p. 399.
Conus ebraeus Linné var. D. Dillwyn, 1817, Descr. Cat. Rec. Shells, p. 399.
Conus hebraeus Linné var. β. Reeve, 1843, Conchol. Icon., 1: pl. 19, fig. 104a.
Conus hebraeus Linné var. *vermiculatus* Lamarck. Kiener, 1846, Spéc. Gén. Icon. Coq. Viv., 2: 46, pl. 8, fig. 3.
Conus ebraeus Linné var. *vermiculatus* Hwass. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 249.
Conus ebraeus Linné var. *vermiculatus* Lamarck. Crosse and Marie, 1874, Jour. Conchyl., 22: 340.
Conus hebraeus Linné var. *vermiculatus* Hwass. Kobelt, 1878, Illus. Conchyl., p. 92.
Conus vermiculatus Bruguière. Fischer, 1891, Bull. Soc. Hist. Nat. Autun, 4: 132.
Conus ebraeus Linné var. *vermiculata* Lamarck. Couturier, 1907, Jour. Conchyl., 55: 126.
Cucullus chaldaeus Bolten. Iredale, 1929, Mem. Queensl. Mus., 9: 282.
Virroconus chaldaeus (Bolten). Cotton, 1945, Rec. Austral. Mus., 8: 236.
Conus chaldeus (Röding). Tinker, 1952, Pacific Sea Shells, p. 44.
Conus chaldens (Röding). Dietrich and Morris, 1953, Nautilus, 67: 17, pl. 4, fig. 19.
Virroconus chaldeus (Röding). Kira, 1955, Coloured Illus. Shells Japan, p. 72.
Stephanoconus chaldeus (Röding). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 10.
Conus ebraeus chaldaeus Röding. Hertlein and Emerson, 1957, Amer. Mus. Novit., No. 1859: 3.

DESCRIPTION: Shell rather small but extremely thick and sturdy. Body whorl transversely striate, the striae obsoletely tuberculate near the base, becoming strongly so near the shoulder; aperture narrow. Shoulder coronate; spire moderately elevated, tuberculate, striate; apex often eroded. Color mostly black, with narrow, irregular, usually interrupted white bands at the shoulder and centrally on the body whorl, the black areas also interrupted by intermittent vertical white streaks. Aperture bluish white, the external color pattern visible at the outer lip. Periostracum rather thin, yellow, translucent. In life, foot black, with a broad central longitudinal tan stripe on the sole. Siphon and rostrum black, tipped with red.

LENGTH: Usually less than 40 mm. A specimen collected by the author at Waikiki, Oahu, measures 44 mm.

TYPE LOCALITY: None.

REMARKS: This species is closely related to *Conus ebraeus* and is regarded as a variety of that species by some recent workers (e.g. Dodge, 1953). It differs from *C. ebraeus* in being generally smaller, having a tuberculate surface, and having the black flammules confluent so as to cover most of the shell. The two species are sympatric over a wide range. Hawaiian specimens are easily distinguishable. In other areas, the two species tend to approach each other more closely morphologically but do not intergrade. Lamarck's (1810) statement that the two species are constantly distinct is correct.

C. chaldaeus occurs most commonly near the outer edge of marine benches. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus circumactis Iredale

Figs. 34 and 35 in Plate 2; Fig. 3

Conus cinctus Swainson, 1822, Zool. Illus., ser. 1, 2: pl. 110. (non *cinctus* Bosc, 1801.)

Conus pulchellus Swainson, 1822, Zool. Illus., ser. 1, 2: pl. 114. (non *pulchellus* Röding, 1798.)

Rhizoconus pulchellus (Swainson). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

(?) *Conus connectens* A. Adams, 1854, Proc. Zool. Soc. Lond., 1854: 136.

Conus circumactis Iredale, 1929, Mem. Queensl. Mus., 9: 281.

Conus hammatus Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 86.

Dauciconus circumactis (Iredale). Cotton, 1945, Rec. South Austral. Mus., 8: 246.

Conus hammatus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.

Leptoconus circumactis (Iredale). Kuroda, 1956, Venus: Jap. Jour. Mal., 19: 73.

DESCRIPTION: Shell rather thin; body whorl slightly concave near the base on the left side, spirally striate with the striae obsolete and impressed toward the shoulder but stronger and with widely spaced low knobs basally. Aperture narrow, widening slightly basally; outer lip thin. Shoulder angular, smooth or

FIG. 3. *Conus circumactis* Iredale. Specimens dredged by C. A. Allen off southern shore of Oahu, 8–60 fathoms Left, 21 × 12 mm.; center, 25 × 13 mm.; right, 34 × 18 mm. Photographs by M. Miyamoto.

extremely obsoletely coronate. Spire low; apex nipplelike, especially in young specimens; whorls finely striate, separated by a deeply impressed suture. Color of body whorl pale yellow or yellowish brown, with large white blotches forming a band at the shoulder and another at the middle; body whorl also encircled by narrow brown lines, which are usually interrupted to form dots and dashes; base violet or pink; interior of aperture bluish or pinkish white. Spire white or pinkish white, sparsely maculated with brown. Periostracum rather thick, yellowish brown and opaque in young specimens, yellow and somewhat translucent in older individuals.

LENGTH: 35 mm.

TYPE LOCALITY: Amboina.

REMARKS: All specimens of *C. circumactis* known from the Hawaiian Islands have been collected by dredging. The holotype of *C. hammatus* Bartsch and Rehder, here considered the juvenile of *C. circumactis*, was dredged off Kauai in about 200 fathoms. C. A. Allen collected thirteen specimens from depths of 8–60 fathoms off the southern shore of Oahu.

Of the other species of *Conus* in Hawaii, *C. vitulinus* is most closely related to *C. circumactis*. The latter can be distinguished by its pale ground color, pink or violet base, and yellowish brown periostracum. *C. circumactis* can be distinguished from *C. litoglyphus* by the narrow interrupted transverse brown lines and the pink or violet base in the former.

Conus distans Hwass *in* Bruguière

Fig. 1 in Plate 1

Conus distans Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 634, pl. 321, fig. 11.
Conus distans Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 38.
Virroconus distans (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 254.
Rhizoconus distans (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 75.
Virgiconus distans (Bruguière). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 291.
Stephanoconus distans (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 16.

DESCRIPTION: Shell large, elongate, slightly concave in profile. Body whorl smooth or encircled with obsolete impressed lines; aperture narrow, the sides parallel. Shoulder coronate; spire short, coronated with obtuse rounded tubercles. Color of body whorl yellowish tan, obsoletely banded with white or pale bluish white at the center and near the shoulder. Tubercles of the spire white, depressed areas between them dark brown. A purplish brown stain usually present near the base. Interior of aperture light violet with a lighter central band, darker violet at the base. The violet of the interior is deeper in juvenile specimens, which are generally more colorful. Periostracum thick, olive green, with transverse rows of tufted ridges on body whorl. In life, foot brown; siphon light tan, mottled with brown; rostrum dark brown, tipped with yellow; tentacles light brown; penis orange.

LENGTH: 120 mm.

TYPE LOCALITY: New Zealand. In error (see Wilkins, 1955: 106).

REMARKS: *C. distans* occurs chiefly at the outer areas of reef platforms and in depths of one or more fathoms.

Conus ebraeus Linné

Fig. 20 in Plate 2

Conus ebraeus Linné, 1758, Syst. Nat., ed. 10, p. 715.
Conus hebraeus Linné. Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 142.
Cucullus ebraeus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 42.
Conus quadratus Perry, 1811, Conchology, pl. 24, fig. 5. (non *quadratus* Röding, 1798.)
Conus hebraeus Hwass. Blainville, 1818, Dict. Sci. Nat., 10: 249.
Conus hebraeus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 170.
Conus hebreus. Montrouzier, 1856, Ann. Soc. Imp. Agr. Lyon, 8: 416.

Coronaxis hebraeus (Linné). Frauenfeld, 1869, Verh. Zool.-Bot. Ges. Wien, 19: 863.
Virroconus ebraeus (Linné). Iredale, 1930, Mem. Queensl. Mus., 10: 80.
Stephanoconus ebraeus (Linné). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 9.

DESCRIPTION: Shell solid; body whorl smooth, becoming encircled with obsolete raised ridges toward the base; outer lip of aperture flaring slightly basally. Shoulder coronate, often obsoletely so; spire of moderate height, often somewhat eroded, indistinctly coronate. Color white with usually three rows of large angular rhomboidal black flammules, with another row encircling the shoulder. Aperture with clouded bands corresponding with the exterior markings. Periostracum thin, yellow, translucent. In life, foot black, with a broad longitudinal central buff stripe on the sole. Siphon and rostrum black, tipped with a narrow red margin.

LENGTH: This species attains greater length in the Hawaiian Islands than in other parts of its extensive range. Specimens exceeding 50 mm. are often found. A specimen collected by the author at Diamond Head, Oahu, measures 56 mm. in length.

TYPE LOCALITY: India.

REMARKS: One of the most abundant species of *Conus* in the Hawaiian Islands, *C. ebraeus* is the dominant species on intertidal benches and occurs also on reef platforms. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus flavidus Lamarck

Fig. 18 in Plate 1

Conus flavidus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 265.
Conus virgo Linné var. Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 362.
Dendroconus flavidus (Lamarck). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.
Conus neglectus Pease, 1860, Proc. Zool. Soc. Lond., pt. 28: 398. (non *neglectus* A. Adams, 1853.)
Conus flavidus Bruguière. Issel, 1869, Malacologia del Mar Rosso, p. 143.
Lithoconus flavidus (Lamarck). Brazier, 1877, Proc. Linn. Soc. New South Wales, 1: 288.
Lithoconus peasei Brazier, 1877, Proc. Linn. Soc. New South Wales, 1: 288.
Conus lividus Hwass var. *flavidus* Lamarck. Smith, 1879, Phil. Trans. Roy. Soc. Lond., 168 (extra volume): 477.
Virgiconus flavidus (Lamarck). Cotton, 1945, Rec. South Austral. Mus., 8: 254.

DESCRIPTION: Shell thick and heavy. Body whorl transversely striate, the striae more pronounced and raised toward the base; aperture narrow. Shoulder rather square, smooth; spire low, striate. Color of body whorl usually olivaceous or yellowish brown banded with white and/or bluish white at the shoulder and below the middle. Base stained dark violet. Aperture violet, with a light central band and yellow margin. Periostracum gray, transversely ridged in young specimens, smooth in older individuals. In life, upper surface of foot reddish brown, mottled with brown; remainder of foot and rostrum light yellowish brown mottled with darker brown; tip of siphon yellow, followed proximally by black and yellow bands; remainder of siphon yellow mottled with black. Tentacles white to yellow.

LENGTH: 50 mm.

TYPE LOCALITY: None.

REMARKS: *C. flavidus* is one of the commonest species of *Conus* on Hawaiian coral reefs. Pleistocene fossils have been collected on Oahu by Ostergaard (1928) and the writer and on Molokai by Ostergaard (1939).

Conus imperialis Linné

Fig. 7 in Plate 1

Conus imperialis Linné, 1758, Syst. Nat., ed. 10, p. 712.
Conus fuscatus Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 126.
Cucullus imperialis (Gmelin). Röding, 1798, Mus. Boltenianum, p. 37.

Cucullus corona-ducalis Röding, 1798, Mus. Boltenianum, p. 38.
Cucullus regius Röding, 1798, Mus. Boltenianum, p. 38. (non *regius* Gmelin, 1791.)
Conus viridulus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 31.
Conus imperialis Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 157–158, figs. 128, 129.
Conus fuscatus Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 157–158, figs. 130, 131.
Conus viridulus Linné. Adams and Adams, 1853, Gen. Rec. Moll., 1: 247.
Conus queketti Smith, 1906, Ann. Natal Govt. Mus., 1: 22, pl. 7, fig. 1.
Cucullus imperialis (Linné). Kira, 1955, Coloured Illus. Shells Japan, p. 72.
Rhombus imperialis (Linné). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 289.

DESCRIPTION: Shell large and sturdy, body whorl elongate, striate basally; outer lip thin. Shoulder coronate; spire low, strongly coronate. Ground color of shell white, with numerous interrupted light and dark brown bands on the spire as well as on the body whorl. Two broad yellowish brown bands encircle the body whorl. The band nearer the shoulder is broader. Both bands contain several narrow revolving dark brown lines interrupted by white. Color of base pale blue, often as narrow interrupted revolving lines. Base of aperture stained with a dark purple marginal band. Periostracum thin, yellow, translucent, but often obscured by epizooic coralline algae in nature. In life, exposed soft parts red, speckled with black.

LENGTH: 90 mm.

TYPE LOCALITY: None.

REMARKS: *C. imperialis* occurs on reef platforms and to a depth of at least 30 fathoms. Pleistocene fossils are known from Oahu (Ostergaard, 1928).

Conus leopardus (Röding)

Fig. 10 in Plate 1

(?) *Conus litteratus* Linné var. β Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 128.
Conus litteratus Linné var. β Born, 1780, Test. Mus. Caes. Vind., p. 149.
Conus litteratus Linné var. D Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 638, pl. 324, fig. 4.
Conus litteratus Linné var. G Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 638, pl. 324, fig. 3.
Conus litteratus Linné var. I Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 638, pl. 323, fig. 5.
Cucullus leopardus Röding, 1798, Mus. Boltenianum, p. 41.
Conus literatus var. B. Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 357.
Conus millepunctatus Lamarck, 1822, Hist. Nat. Anim. sans Vert., 7: 461. (non *millepunctatus* Röding, 1798.)
Conus litteratus Linné var. *millepunctatus* Lamarck. Anton, 1839, Verzeichniss, p. 105.
Conus mille punctatus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 167.
Conus millepunctatus Linné. Mörch, 1852, Catal. Conchyl. Yoldi, p. 66.
Dendroconus millepunctatus (Lamarck). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.
(?) *Leptoconus leopardus*. Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.
Conus millepunctatus Bruguière. Sowerby, 1857, Thes. Conchyl., 3: 23, pl. 7, fig. 151.
Conus millipunctatus Lamarck. Theobald, 1860, Catal. Rec. Sh. Mus. Asiat. Soc. Bengal, p. 23.
Conus literatus Linné var. *millepunctatus* Lamarck. Tryon, 1884, Man. Conch., 6: 10, pl. 2, fig. 19.
Conus millepunctatus Hwass. Von Martens and Thiele, 1903, Beschr. Gastrop. Deutsche Tiefsee Exp., p. 136.
Cucullus pardus Bolten. Iredale, 1929, Mem. Queensl. Mus., 9: 282. (error. *pardus* Röding, 1798 = *litteratus* Linné, 1758.)
Conus litteratus Linné var. *millepunctata* Lamarck. Dautzenberg and Bouge, 1933, Jour. Conchyl., 77: 78.

Conus millepunctatus Lamarck var. *aldrovandi* Dautzenberg, 1937, Mém. Mus. Roy. Hist. Nat. Belg., 2(18): 171. (non *aldrovandi* Risso, 1826.)
Conus litteratus pardus (Bolten). Suvatti, 1938, Molluscs of Siam, p. 39.
Conus litteratus pardus (Röding). Kira, 1955, Coloured Illus. Shells Japan, p. 72.
Lithoconus leopardus (Röding). Kaicher 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 13.

DESCRIPTION: Shell massive, conical. Body whorl with very obscure striae; base truncate; aperture rather narrow, the sides parallel. Shoulder smooth; spire depressed, spirally canaliculate and striate. Color of body whorl cream white, with many encircling rows of oblong bluish brown to black spots. One or two rows of small spots often alternate with one or two rows of large ones. The spots are more pronounced in smaller individuals. The body whorl of juvenile specimens is dark cream with narrow transverse white bands on which the dark spots are superimposed. The latter are more square than in adult specimens. Specimens 15 cm. or more in length may be almost completely unmarked. Color of aperture white or pale orange, sometimes yellow at the base. Periostracum olive brown, very thick, opaque. In life, exposed soft parts yellowish white, mottled with brown.

LENGTH: Ordinarily 150–200 mm. This species is the largest representative of the genus in Hawaii. A specimen in the collection of Mr. C. S. Weaver of Honolulu measures 221 × 124 mm.

TYPE LOCALITY: None.

REMARKS: *Conus leopardus* may be distinguished from *C. litteratus* Linné, its closest relative, by the following characteristics: *C. litteratus*, which does not occur in Hawaii, attains a length of only about 5 inches. It generally reaches its maximum width anterior of the shoulder, rather than at the shoulder, as in *C. leopardus*. The base of *C. litteratus* is pointed rather than truncate, and it typically bears a black smudge at the base of the aperture. The spots are more nearly similar in size and more square, and the shell typically bears two broad yellow bands.

C. leopardus is occasionally found on reef platforms but occurs more commonly in depths of one fathom or more in bays and offshore. It is known to occur to a depth of 12 fathoms. Pleistocene fossils of *C. leopardus* are known from Oahu (Ostergaard, 1928).

Conus litoglyphus Hwass *in* Bruguière

Conus capitaneus var. δ. Gmelin, 1791, Syst. Nat., ed. 13, p. 3377.
Conus capitaneus var. ζ. Gmelin, 1791, Syst. Nat., ed. 13, p. 3377.
Conus litoglyphus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 692, pl. 338, fig. 8.
Cucullus cinamomeus Röding, 1798, Mus. Boltenianum, p. 43.
Cucullus orleanus Röding, 1798, Mus. Boltenianum, p. 44.
Conus subcapitaneus Link, 1807, Beschr. Nat.-Samml. Univ. Rostock, Abt. 3, p. 103.
Conus lithoglyphus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 280.
Conus lithoglyphus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 175.
Conus lacinulatus Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 108, fig. 2, p. 312.
Conus carpenteri Crosse, 1865, Jour. Conchyl., 13: 302, pl. 9, fig. 1.
(?) *Conus seychellensis* Nevill, 1874, Jour. Asiatic Soc. Bengal, 43(2): 22.
Conus lithoglyphus Reeve. Tomlin, 1937, Proc. Malac. Soc. Lond., 22: 268.
Dauciconus ermineus (Born). Cotton, 1945, Rec. South Austral. Mus., 8: 246.
Conus lithographus. Platt, 1949, Natl. Geog. Mag., 96: 53, fig. 2.
Conus inermis Born. Tinker, 1952, Pacific Sea Shells, p. 40.
Lithoconus ermineus (Born). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 4, fig. 10.

DESCRIPTION: Shell elongate; body whorl faintly and distantly striate toward the base,

the striae obsolutely tuberculate. Aperture very narrow, the sides parallel. Color of body whorl dull yellow, reddish brown, or chestnut, often darker at the base, banded at the center and shoulder with rows of white blotches. Spire with alternate brown and white maculations on each whorl. Interior of aperture white.

LENGTH: 50 mm.

TYPE LOCALITY: "Mers des grandes Indes."

REMARKS: This species has often been referred to as *Conus ermineus* Born (Dautzenberg, 1937). Although Born did not provide a figure of *C. ermineus* and his brief description has been held by some (Burch, 1955) to be inadequate, the first figure reference given by Born (Valentyn, 1773: pl. 5, fig. 47) is a fairly good representation of the species under discussion. However, as was first pointed out by Brauer (1878), the two specimens on which Born's original description was based (Naturhistorisches Museum, Vienna, Nos. 4051 and 4052) are not conspecific with *C. litoglyphus* Hwass. Born's specimens are of the species later described by Lamarck (1810: 281) as *C. narcissus*.

Conus litoglyphus occurs rarely on Hawaiian reefs. It has been collected at a depth of 30 fathoms.

Conus lividus Hwass *in* Bruguière

Fig. 17 in Plate 1

Conus rusticus var. *β* Gmelin, 1791, Syst. Nat., ed. 13, p. 3383. (non *rusticus* Linné, 1758.)

Conus lividus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 630, pl. 321, fig. 5.

Conus rusticus Linné (Gmelin). Schreibers, 1793, Conchylienkenntniss, 1: 26.

Cucullus monachos Röding, 1798, Mus. Boltenianum, p. 39.

Conus plebejus Link, 1807, Beschr. Nat.-Samml. Univ. Rostock, Abt. 3, p. 106.

Conus lividus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 36.

(?) *Conus balteatus* Sowerby, 1833, Conch. Illus., p. 3, pt. 37, fig. 58.

Conus lividus Lamarck. Quoy and Gaimard, 1834, Voy. *Astrolabe* Zool., 3: 98, pl. 53, figs. 19–21.

Conus sanguinolentus Quoy and Gaimard, 1834, Voy. *Astrolabe* Zool., 3: 99, pl. 53, fig. 18.

Conus lividus Linné. Krauss, 1848, Die Südafrikanischen Molluscen, p. 130.

Conus rusticus Linné. Mörch, 1857, Catal. Suenson, p. 32. (error).

Conus citrinus Gmelin. Sowerby, 1857, Thes. Conchyl., 3: 4, pl. 4, fig. 70. (error).

(?) *Conus bocki* Sowerby, 1881, Proc. Zool. Soc. Lond., 1881: 636, pl. 56, fig. 7.

(?) *Conus prytanis* Sowerby, 1882, Proc. Zool. Soc. Lond., p. 117, pl. 5, fig. 1.

Conus plebeius Link. Tomlin, 1937, Proc. Malac. Soc. Lond., 22: 293.

Virgiconus lividus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 254.

Rhizoconus lividus (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 75.

Stephanoconus lividus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 13.

DESCRIPTION: Shell solid, with widely spaced transverse slightly elevated striae on the body whorl, the striae obsolete near the shoulder but strongly granulated basally. Aperture narrow, the sides parallel. Shoulder coronate; spire obtuse, coronated with large tubercles, striate, often eroded. Color olivaceous or orange brown, with tubercles of the spire and a transverse band below the shoulder white or bluish white. A central band on the body whorl light yellow, white, or bluish white. Color of aperture violet with a pale central transverse band; margin of outer lip yellow. Periostracum greenish brown, thick, opaque. In life, foot, rostrum and siphon black, finely mottled with more or less red, appearing reddish black.

LENGTH: Usually to 60 mm. A specimen 76 mm. in length, collected near Nanakuli, Oahu, is in the collection of Mr. A. M. Harrison of Honolulu.

TYPE LOCALITY: "Antilles," "Isle-de-France

& aux Indes orientales." The first locality is undoubtedly in error. Île de France was an eighteenth-century French name for Mauritius, which was probably the source of Hwass's specimens.

REMARKS: *C. lividus* is one of the two most abundant species of *Conus* on Hawaiian coral reef platforms, the other being *C. flavidus*.

Conus marmoreus Linné

Fig. 9 in Plate 1

Conus marmoreus Linné, 1758, Syst. Nat., ed. 10, p. 712.
Conus nocturnus Solander, 1786, Cat. Portland Mus., p. 156, no. 3411.
Conus marmoratus Linné. Herbst, 1788, Hist. Verm., p. 176, pl. 43, fig. 1. (Not seen.)
Conus bandanus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 611, pl. 318, fig. 5.
Conus nocturnus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 611, pl. 318, fig. 1.
[*Conus tigrinus* Humphrey, 1797, Mus. Calonnianum, p. 13.]
[*Conus nigritus* Humphrey, 1797, Mus. Calonnianum, p. 13.]
Cucullus marmoreus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 38.
Cucullus proarchithalassus Röding, 1798, Mus. Boltenianum, p. 38.
Conus proarchithalassius (Bolten). Link, 1807, Beschr. Nat.-Samml. Univ. Rostock, Abt. 3, p. 105.
Conus marmoreus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 29.
Conus bandanus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 29.
Conus nocturnus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 30.
Conus maculatus Perry, 1811, Conchology, pl. 24, fig. 4.
Conus bandanus Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 155–156, fig. 121.
Conus nocturnus Lamarck. Sowerby, 1839, Conch. Illus., p. 4, pt. 155–156, figs. 122, 123.
Coronaxis bandanus (Lamarck). Swainson, 1840, Treatise on Malacol., p. 311.
Conus proarchithalassus (Bolten). Mörch, 1852, Catal. Conchyl. Yoldi, p. 64.
Conus deburghiae Sowerby, 1857, Thes. Conchyl., 3: 2, pl. 1, figs. 6, 7.
Conus nigrescens Sowerby, 1859, Proc. Zool. Soc. Lond., pt. 27: 429, pl. 49, fig. 2.
Conus crosseanus Bernardi, 1861, Jour. Conchyl., 9: 168, pl. 6, figs. 5, 6.
Conus pseudomarmoreus Crosse, 1875, Jour. Conchyl., 23: 223, pl. 9, fig. 4.
Conus marmoreus bandanus Hwass. de Burros e Cunha, 1933, Mem. Estud. Mus. Zool. Univ. Coimbra, Sér. 1, No. 71: 10.
Coronaxis bandanus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 235.
Cucullus marmoreus (Linné). Kira, 1955, Coloured Illus. Shells Japan, p. 72.
Cucullus bandanus (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 72.
Conus marmoreus bandanus Lamarck. Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 3, fig. 6.

DESCRIPTION: Shell large; body whorl obsoletely striate, its maximum diameter slightly anterior of the shoulder; aperture rather narrow, with almost parallel margins. Shoulder strongly coronate; spire depressed, coronate, striate. Large triangular pale flesh-colored markings separated by dark brown and crowded in two areas form broad irregular bands on the body whorl in specimens from the Hawaiian Islands, the anterior band being narrower. Aperture white or pale pink. Periostracum thin, yellow, translucent. In life, foot tan, siphon banded proximally from the tip with red, white, and black bands.

LENGTH: Usually to 100 mm. A specimen from Oahu in the B. P. Bishop Museum measures 139 mm.

TYPE LOCALITY: Asia.

REMARKS: Hawaiian representatives differ from typical *C. marmoreus*, in which the white markings are larger and less crowded and do not form bands. In some localities, such as New Caledonia (Crosse and Marie, 1874),

Bikini, the Philippines, both forms occur together, with intergrades. To the writer's knowledge, none of the typical forms of *C. marmoreus* have ever been collected in the Hawaiian Islands. The form found in Hawaii (and elsewhere) was described as *C. bandanus* Hwass *in* Bruguière. Most authorities regard the latter as a variety of *C. marmoreus*, which is probably valid in areas where both, as well as intergrades, occur. However, it is probably legitimate to consider the Hawaiian populations as belonging to the subspecies *Conus marmoreus bandanus* Hwass *in* Bruguière. It occurs uncommonly on Hawaiian reefs and has been collected at a depth of eight fathoms.

Conus miles Linné

Fig. 6 in Plate 1

Conus miles Linné, 1758, Syst. Nat., ed. 10, p. 713.
Cucullus miles (Gmelin). Röding, 1798, Mus. Boltenianum, p. 43.
Conus miles Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 171.
Leptoconus miles (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.
Rhizoconus miles (Linné). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.
Lithoconus miles (Linné). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 3.

DESCRIPTION: Shell solid, with a moderately elevated spire. Body whorl smooth except for raised granular transverse ridges near the base. Aperture narrow, the sides parallel; outer lip thin. Shoulder obsoletely coronate; spire obsoletely tuberculate or plicate, rather faintly striate, concave in young individuals to straight or convex in larger ones. Color of body whorl yellowish white, with a broad, transverse blackish brown band above the center of the body whorl, and another at the base. The bands may be divided transversely into lighter and darker portions. Above and below the upper band, shell marked by narrow threadlike longitudinal dark brown lines, which are continuous on the spire; the lines becoming more closely spaced in older individuals. The broad brown bands, alternating with white, are visible within the aperture. Periostracum greenish brown, with transverse rows of tufted ridges on the body whorl. In life, exposed soft parts greenish black.

LENGTH: 80 mm.

TYPE LOCALITY: India.

REMARKS: *C. miles* is rare on Hawaiian coral reefs and marine benches but occurs more commonly at depths of one to several fathoms. It has been collected at a depth of 26 fathoms.

Conus moreleti Crosse

Fig. 16 in Plate 1

Conus elongatus Reeve, 1843, Conch. Icon., 1: pl. 27, fig. 157. (non *elongatus* Borson, 1820.)
Conus oblitus Reeve, 1849, Conch. Icon., 1(Emendns.): 1. (non *oblitus* Michelotti, 1847.)
Conus moreleti Crosse, 1858, Rev. Mag. Zool., Ser. 2, 10: 122.
Conus lividus Hwass var. *elongatus* Reeve. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 262.
Conus lividus Bruguière var. *moreleti* Crosse. Paetel, 1887, Catal. Conch.-Samml. Paetel, 1: 299.
Stephanoconus moreleti (Crosse). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 14.

DESCRIPTION: Shell elongate, body whorl with raised, obsoletely knobbed striae basally, otherwise smooth; aperture very narrow, the sides parallel; outer lip thin. Shoulder coronate; spire low, convex, coronate, striate. Color of body whorl yellowish brown or olive, darker at the base, with lighter transverse bands at the shoulder and at the middle. Interior of aperture deep violet, outer lip yellow. Periostracum yellowish brown, rather thin, translucent, forming tufts on the tubercles.

LENGTH: 50 mm.

REMARKS: *C. moreleti* may be distinguished from *C. lividus*, its closest relative, by its elongate shape and small and closely spaced tubercles on the shoulder. It is rare on Hawaiian reefs but occurs more commonly at depths of a few fathoms.

Conus nussatella Linné

Fig. 19 in Plate 1

Conus nussatella Linné, 1758, Syst. Nat., ed. 10, p. 716.
Conus mussatellana Linné. Schröter, 1782, Mus. Gottwald., p. 23, pl. 13, figs. 96^a, 96^b, 96^c; pl. 43, fig. 52^a.
[*Conus punctulatus major* Humphrey, 1797, Mus. Calonnianum, p. 15.]
Cucullus nussatella (Gmelin). Röding, 1798, Mus. Boltenianum, p. 50.
Hermes nussatellus (Linné). Montfort, 1810, Conchyl. Syst., 2: 399.
Coni nussatellae Linné. Müller, 1836, Synopsis Nov. Gen. Spec. Var. Testaceorum Viventum, p. 122.
Conus nussatella Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 178.
Hermes nussatula (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 256.
Conus nusatella Linné. Mörch, 1854, Catal. Hencks, p. 21.
Conus nusatella Linné. Weinkauff, 1873, Syst. Conch. Cab., ed. 2, 4: 151.
Hermes nussatella Linné. Schmeltz, 1874, Catal. Mus. Godeffroy, 5: 136.
Hermes nusatellata (Linné). Brazier, 1877, Proc. Linn. Soc. New South Wales, 1: 291.
Conus nussatellata Linné. Brazier, 1879, Jour. Conchol., 2: 192.

DESCRIPTION: Shell cylindrical, rather thin. Body whorl closely striate, the striae minutely granular. Aperture narrow, flaring slightly basally. Shoulder rounded; spire high, convex; apex sharp. Color yellowish white, clouded irregularly with orange brown or light purplish brown longitudinal splotches; with transverse rows of numerous small dark orange brown spots on the body whorl and spire. Periostracum thin, yellow, translucent.

LENGTH: 60 mm.

TYPE LOCALITY: "Nussatello Insulam Asiae."

REMARKS: *C. nussatella* is a rare species in the Hawaiian Islands. Pleistocene fossils have been collected on Oahu by Ostergaard (1928) and the writer.

Conus obscurus Sowerby

Fig. 36 in Plate 2

Conus obscurus Sowerby, 1833, Conch. Illus., p. 2, pt. 29, fig. 26.
Conus obscurus Humphreys MSS. Reeve, 1843, Conch. Icon., 1: pl. 16, fig. 82.
Conus obscurus Reeve. Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 68, fig. 2, p. 347.
Nubecula obscura (Humphreys). Adams and Adams, 1853, Gen. Rec. Moll., 1: 249.
Conus tulipa Linné, juv. Pease, 1868, Am. Jour. Conch., 4: 126. (error).
Conus obscurus (Hwass) Reeve. Dautzenberg, 1937, Mém. Mus. Roy. Hist. Nat. Belg., 2: 193, pl. 3, fig. 9.
Conus halitropus Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 88.
Conus halitropus Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.
Tuliparia obscura (Reeve). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 291.
Gastridium obscurum (Sowerby). Kuroda, 1956, Venus: Jap. Jour. Mal., 19: 80.

DESCRIPTION: Shell elongate-ovate, very thin. Body whorl smooth except for very fine transverse grooves basally. Aperture rather broad, flaring basally. Shoulder smooth; spire moderately elevated, striate; apex pointed. Shell marked by irregularly shaped and distributed blotches and dots of light brown; the lighter areas separating them are violet. Periostracum very thin, translucent.

LENGTH: 30 mm.

TYPE LOCALITY: Arabia.

REMARKS: *C. obscurus* occurs rarely in shal-

low water in Hawaii and is apparently more common at depths of several fathoms.

Conus pennaceus Born

Fig. 3 in Plate 1

Conus pennaceus Born, 1780, Test. Mus. Caes. Vind., p. 167, pl. 7, fig. 14.
Conus aulicus var. α Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.
Conus aulicus var. β Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.
Conus aulicus var. γ Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.
Conus aulicus var. ϵ Gmelin, 1791, Syst. Nat., ed. 13, p. 3394.
(?) *Conus omaria* Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 743, pl. 344, fig. 3.
Conus rubiginosus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 746, pl. 344, figs. 1, 2.
(?) *Conus praelatus* Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 746, pl. 345, fig. 4.
(?) *Conus episcopus* Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 748, pl. 345, figs. 2, 6. (In part.)
(?) *Conus crocatus* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 424.
(?) *Conus colubrinus* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 433.
Conus pennaceus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 434.
Conus omaria Hwass var. β. Reeve, 1843, Conch. Icon., 1: pl. 32, sp. 177, figs. 177a, 177b.
Conus pennaceus Lamarck. Reeve, 1843, Conch. Icon., 1: pl. 32, sp. 177.
(?) *Conus elisae* Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 64, figs. 1, 1a, p. 341.
(?) *Conus stellatus* Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 99, fig. 3, p. 225.
Conus madagascariensis Sowerby, 1858, Thes. Conchyl., 3: 43, pl. 24, fig. 582.
Conus racemosus Sowerby, 1873, Proc. Zool. Soc. Lond., 1873: 721, pl. 59, fig. 11.
Conus auratus Hwass. Ostergaard, 1928, Bull. Bishop Mus., 51: 4, 29. (error).
Darioconus racemosus (Sowerby). Cotton, 1945, Rec. South Austral. Mus., 8: 257.
Darioconus pennaceus (Born). Cotton, 1945, Rec. South Austral. Mus., 8: 257.
Conus auratus Hwass. Morris, 1952, Field Guide to Shells Pac. Coast & Hawaii, p. 202, col. pl. 7, fig. 3. (error).
Cylinder pennaceus (Born). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 7, fig. 13.

DESCRIPTION: Shell ventricose, robust, broad at the shoulder; maximum diameter equal to or greater than one half the shell length. Body whorl obsoletely striate, the striae more pronounced basally. Aperture rather broad, flaring slightly basally. Shoulder smooth, usually somewhat rounded, but variable. Spire variable, depressed to moderately elevated, concave to slightly convex, obsoletely striate; protoconch nipplelike, rose colored. Ground color reddish brown (yellow specimens are occasionally found), with narrow transverse closely spaced lines, finely dotted with white. These areas are interrupted by large white subtrigonal blotches, grouped together like scales, usually forming a central band and sometimes additional bands at the shoulder and base. Color pattern of the body whorl usually continued on the spire. Interior of aperture white or bluish white. In life, foot pale brown mottled with darker brown; tip of siphon vermillion, followed proximally by white and black bands.

LENGTH: Usually to 65 mm. A specimen in the U. S. National Museum, collected at Hilo, Hawaii, measures 82 mm. in length.

TYPE LOCALITY: China.

REMARKS: Most specimens found in Hawaii agree fairly well with the original description and figure, although there is considerable morphological variation.

C. pennaceus is extremely similar to *C. omaria* Hwass *in* Bruguière. Tryon (1884) and some other authors have synonymized the two. Kiener (1849–1850: 340) listed characteristics by which the two species may be distinguished, stating under *C. pennaceus*, "C'est avec le *Conus omaria* que cette espèce a le plus d'analogie; le système de coloration de ces deux coquilles est à peu près semblable;

seulement, dans l'espèce ici décrite, les grandes zones sont plutôt longitudinales que transverses, et le réseau qui les constitue n'est pas aussi nettement limité. La form d'ailleurs est également différente; elle est toujours plu raccourcies et plue ventrue." The present writer has found that these distinctions generally hold, but it would be difficult to classify a small percentage of specimens collected in Hawaii using these criteria. If the two species eventually prove to be synonymous, the name *C. pennaceus* has priority over *C. omaria*.

C. pennaceus is one of the most common species on Hawaiian coral reef platforms. Fossils are known from Pleistocene deposits on Molokai (Ostergaard, 1939, as *C. omaria*).

C. elisae Kiener, here listed questionably as a synonym, is possibly a valid species. For an account of it, see page 396.

Conus pertusus Hwass *in* Bruguière

Fig. 31 in Plate 2

Conus nobilis Linné. Schröter, 1783, Einl. Conchyl., 1: 36, pl. 1, fig. 4. (error).
Conus pertusus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 686, pl. 336, fig. 2.
Conus pertusus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 278.
Conus amabilis Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 425.
Conus festivus Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 413.
(?) *Conus inquinatus* Reeve, 1849, Conch. Icon. Suppl., pl. 5, sp. 251.
Hermes pertusus (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 256.
Conus pertusus Lamarck. Sowerby, 1858, Thes. Conchyl., 3: 23, pl. 13, fig. 273.
Leptoconus pertusus. Schmeltz, 1874, Catal. Mus. Godeffroy, 5: 136.
Pionoconus pertusus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 249.
Rhizoconus pertusus (Bruguière). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 290.
Lithoconus pertusus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 4.

DESCRIPTION: Shell conical; body whorl encircled by distantly spaced punctate striae; aperture rather narrow, sides parallel. Shoulder smooth; spire low, convex, rather obtuse. Color rose, flaked with yellow or white, banded with two interrupted transverse rows of white or light pink blotches below the shoulder and centrally on the body whorl.

LENGTH: 40 mm.

TYPE LOCALITY: "Grandes Indes."

REMARKS: *Conus pertusus* is uncommon in Hawaii. It is known to occur subtidally to a depth of 25 fathoms.

Conus pulicarius Hwass *in* Bruguière

Fig. 12 in Plate 1

Conus pulicarius Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 622, pl. 320, fig. 2.
Conus fustigatus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 623, pl. 320, fig. 1.
Cucullus punctulatus Röding, 1798, Mus. Boltenianum, p. 40.
Conus pulicarius Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 34.
Conus fustigatus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 35.
Conus pulicarius Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 174.
Conus vautieri Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 100, fig. 3, p. 350.
Conus fustigatus Lamarck. Reeve, 1849, Conch. Icon. Temp. Index (Critical Analysis), unpaginated.
Puncticulis pulicarius (Hwass). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.
Puncticulis pulicarius (Bruguière). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 289.

DESCRIPTION: Shell thick and solid; body whorl with impressed transverse striae basally; aperture rather narrow, sides parallel. Shoulder coronate; spire moderately elevated, striate, coronate. Color white with dark brown to black spots, the spots often crowded into two transverse bands, one on each side of the center. Spire white, marked sparingly with

brown dots. Periostracum yellow, very thin and translucent in young individuals, thicker and brown in larger specimens. In life, foot and rostrum pale tan mottled with yellowish to reddish brown; tip of siphon reddish orange, followed proximally by pale buff and black bands.

LENGTH: Usually to 60 mm. A specimen collected by W. H. Christensen at Ala Moana Reef, Oahu, measures 74 × 42 mm. A specimen collected by C. S. Weaver measures 73 × 44 mm.

TYPE LOCALITY: Pacific Ocean.

REMARKS: *C. pulicarius* occurs in patches of sand on reef platforms and in bays. It has been collected at depths exceeding 40 fathoms.

Conus quercinus Solander

Fig. 4 in Plate 1; Fig. 23 in Plate 2

Conus quercinus Solander *in* Cat. Portland Mus., 1786, p. 67, no. 1501.
Conus cingulum Gmelin, 1791, Syst. Nat., ed. 13, p. 3378.
Conus quercinus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 681, pl. 332, figs. 5, 6.
Conus quercinus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 276.
Conus guercinus Hwass. Blainville, 1818, Dict. Sci. Nat., 10: 249.
Conus quercinus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 172.
Dendroconus quercinus (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.
Conus ponderosus Sowerby, 1858, Thes: Conchyl., 3: 54.
Lithoconus quercinus (Bruguière). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.
Cleobula quercina (Solander). Cotton, 1945, Rec. South Austral. Mus., 8: 260.
Lithoconus quercinus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 9.

DESCRIPTION: Shell large and solid, variable in obesity. Body whorl obsoletely striate, the striae becoming more pronounced basally; aperture rather wide, sides parallel. Shoulder smooth, rounded. Spire depressed, concave, striate; apex raised. Color of body whorl yellow, encircled with numerous closely spaced transverse threadlike brown lines; spire usually paler yellow; interior of aperture white. Periostracum thick, brown, opaque. In life, foot and siphon brownish gray, heavily speckled with black.

LENGTH: Usually to 100 mm. A specimen from Oahu in the B. P. Bishop Museum measures 134 mm.

TYPE LOCALITY: None.

REMARKS: *C. quercinus* is found in large sandy areas in bays and to depths of more than 40 fathoms.

Conus rattus Hwass *in* Bruguière

Fig. 30 in Plate 2

Conus rattus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 700, pl. 338, fig. 7.
Conus taitensis Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 713, pl. 336, fig. 9.
Conus capitaneus var. C. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 266.
Conus rattus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 408.
Conus taitensis Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 424.
Conus capitaneus var. B. Küster, 1837–1840, Syst. Conch. Cab., ed. 2, 4: 8, pl. 14, figs. 13, 14.
Conus taheitensis Hwass. Reeve, 1843, Conch. Icon., 1: pl. 15, sp. 78.
Conus rattus Lamarck. Reeve, 1843, Conch. Icon., 1: sp. 78.
Conus taheitensis Hwass var. *rattus* Lamarck. Catlow and Reeve, 1845, Conchol. Nomencl., p. 322.
Leptoconus rattus (Lamarck). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.
Leptoconus taheitensis (Hwass). Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.
Conus taheitensis Bruguière. Sowerby, 1857, Thes. Conchyl., 3: 5, pl. 2, fig. 26.

Conus viridis Sowerby, 1857, Thes. Conchyl., 3: 20, pl. 5, fig. 102.
Conus tahitiensis Bruguière. Schmeltz, 1865, Catal. II Godeffroy, p. 20.
Conus rattus Solander. Schaufuss, 1869, Molluscorum Syst. Cat. Paetel, p. 45.
Conus tahitensis Bruguière. Schaufuss, 1869, Molluscorum Syst. Cat. Paetel, p. 45.
Conus ratus var. *tahitensis*. Ostergaard, 1928, B. P. Bishop Mus. Bull. 51: 29.
Conus tahitiensis Hwass (emend.). Dautzenberg and Bouge, 1933, Jour. Conchyl., 77: 89.
Rhizoconus rattus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., vol. 8, p. 252.
Conus tahitensis Hwass. Mermod, 1947, Rev. Suisse Zool., 54: 208.
Lithoconus rattus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 1.

DESCRIPTION: Shell of moderate thickness; body whorl obsoletely striate near the shoulder, but distinctly so near the base, the striae closely spaced; aperture rather narrow, sides nearly parallel. Shoulder angular, smooth; spire rather low, obtuse, striate. Color of body whorl yellowish or violet brown, with large bluish white spots and maculations forming an interrupted central band and another at the shoulder. Shell below central band densely flecked with white, above band sparsely flecked with white. Spire with alternate brown and white blotches, continuing to form band on body whorl at shoulder. Aperture violet within. Periostracum thin, yellow, translucent, smooth or with raised ridges near growing edge. In life, foot, rostrum and siphon dark olive green, mottled with black.

LENGTH: Usually to 40 mm. A specimen collected by T. H. Richert on windward Oahu, and presently in the collection of the Children's Museum of Honolulu, measures 60 mm.

TYPE LOCALITY: "Mers d'Amerique," undoubtedly in error.

REMARKS: *C. rattus* occurs not uncommonly both on intertidal benches and on subtidal reef platforms. Pleistocene fossils are known from Oahu (Ostergaard, 1928) and Maui (Ostergaard, 1939).

Conus retifer Menke

Fig. 32 in Plate 2

Conus retifer Menke, 1829, Verz. Ans. Conch.-Samml. Malsburg, p. 68.
Conus solidus Sowerby, 1834, Conch. Illus., p. 3, pt. 56, fig. 76. (non *solidus* Gmelin, 1791.)
Cylinder solidus (Sowerby). Adams and Adams, 1853, Gen. Rec. Moll., 1: 255.
Darioconus retifer (Menke). Cotton, 1945, Rec. South Austral. Mus., 8: 258.
Cylinder retifer (Menke). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 7, fig. 10.

DESCRIPTION: Shell very thick and solid, pear-shaped. Body whorl striate; aperture with almost parallel sides. Shoulder rounded, smooth. Spire elevated, acuminated, striate. Color reticulated orange brown with large and small white triangular markings, arranged as scales, and longitudinal chocolate and orange markings mostly interrupted to form two transverse bands. Color pattern of body whorl continued on spire; apex pink. Interior of aperture white or pale pink. Periostracum very thin, pale yellow, very translucent. In life, foot mottled brown. Tip of siphon vermillion, followed proximally by white and black bands.

LENGTH: 50 mm.

TYPE LOCALITY: None.

REMARKS: *C. retifer* is uncommon in Hawaii.

Conus spiceri Bartsch and Rehder

Fig. 8 in Plate 1

Conus spiceri Bartsch and Rehder, 1943, Proc. Biol. Soc. Wash., 56: 87.
Conus spiceri Dall, Bartsch and Rehder. Greene, 1953, Ann. Rept. Amer. Malacol. Union, Bull. 20: 28.

DESCRIPTION: Shell large and thick; body whorl marked by fine incremental lines and closely spaced spiral threads, becoming heav-

ier and more distantly spaced basally. Aperture fairly broad, widening somewhat basally. Shoulder broad, smooth, angular. Spire low, concave, singly striate. Color pale yellow, somewhat darker basally, with obscure white transverse bands. Interior of aperture bluish white. Periostracum thick, yellowish brown.

LENGTH: 110 mm.

TYPE LOCALITY: Midway Island.

REMARKS: This species, which is rather rare, is distinguished from *C. quercinus* in that it lacks the brown spiral lines, has a flatter spire, and is only singly striate on the summit. It is distinguished from *C. distans* by lacking the brown bands and tuberculate shoulder. Its closest relative is *C. virgo* Linné, which does not occur in Hawaii. *C. virgo* is easily distinguished from *C. spiceri* by the pronounced violet color of the base in the former.

To the author's knowledge, no specimens of *C. spiceri* have been collected outside the Hawaiian Islands.

Conus sponsalis Hwass *in* Bruguière

Figs. 38 and 39 in Plate 2

Conus sponsalis Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 635, pl. 322, fig. 1.

(?) *Conus ceylanensis* Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 636, pl. 322, fig. 10.

Conus sponsalis Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 38.

Conus nanus Sowerby, 1833, Conch. Illus., p. 1, pt. 24, fig. 6.

Conus nanus Broderip, 1833, Proc. Zool. Soc. Lond., 1833: 53.

Coronaxis nanus (Broderip). Adams and Adams, 1853, Gen. Rec. Moll., 1: 248.

Coronaxis sponsalis. Adams and Adams, 1853, Gen. Rec. Moll., 1: 248.

Conus sponsalis Solander. Von Martens and Langkavel, 1871, Donum Bismarckianum. Samml. Südsee-Conchyl., p. 31.

Conus ceylonensis Hwass var. *sponsalis*. Tryon, 1884, Man. Conch., 6: 23, pl. 6, fig. 99.

Conus ceylonensis Hwass var. *nanus* Broderip. Tryon, 1884, Man. Conch., 6: 24, pl. 6, fig. 100.

Conus nana Broderip. Paetel, 1887, Catal. Conch.-Samml. Paetel, 1: 302.

Conus ceylanensis Hwass var. *pusillus*. Mant, 1922, Nautilus, 35: 84.

Conus ceylonensis Hwass. Ostergaard, 1935, B. P. Bishop Mus. Bull., 131: 21.

Virroconus sponsalis (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 237.

Stephanoconus sponsalis (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, fig. 5.

DESCRIPTION: Shell small but thick and solid, extremely variable with respect to several characteristics. Body whorl usually obsoletely striate, the striae somewhat more pronounced basally; aperture narrow, the sides parallel. Shoulder coronated with small tubercles which may be obsolete in large specimens. Spire usually moderately elevated, inner whorls coronated, but often eroded; 0–3 striae per whorl. Ground color of basal two thirds of body whorl typically pale blue; remaining area near the shoulder white; base tipped with brownish purple. In many specimens, no other coloration is present. Some individuals, chiefly younger specimens, marked with reddish or orange brown on body whorl; these markings generally of two arrangements, one or both of which may be present on the same shell: (1) encircling narrow bands of rather distantly separated dots or dashes separated by white dashes (Fig. 39); (2) interrupted longitudinal blotches of color (Fig. 38). Tubercles white, areas between them sometimes orange brown. Interior of aperture dark violet to brown, with white bands near the shoulder and centrally; outer lip white. Periostracum thin, translucent, sometimes becoming thicker and opaque at the growing edge, or in larger specimens. In life, foot pale pink, mottled with white, darker pink at extremities. Siphon and rostrum pale pink or white, tipped with darker pink; tentacles white.

LENGTH: To 30 mm. Most specimens smaller.

TYPE LOCALITY: "Île Saint-George."

REMARKS: Specimens from Hawaiian populations agree with the original figure and Broderip's (1833) description of *Conus nanus*, which has not generally been considered a distinct species. A number of workers (Pease, 1868; Tryon, 1884; Ostergaard, 1935; Tomlin, 1937; Tinker, 1952) have considered *C. nanus* to be not specifically distinct from *C. ceylanensis*.

C. ceylanensis does not seem to be a well-known species. Specimens from many Indo-West Pacific localities in the U. S. National Museum and Museum of Comparative Zoology collections are indistinguishable from representatives of the Hawaiian populations under consideration.

Examination of specimens from many Indo-West Pacific island groups in the U. S. National Museum, Museum of Comparative Zoology, and Academy of Natural Sciences of Philadelphia, and personal observations of the writer in the Marshall Islands led to the conclusions that the widespread *C. sponsalis* is also extremely variable and that there is sufficient morphological overlap with the Hawaiian forms for the latter to be considered conspecific with *C. sponsalis*. However, since most Hawaiian specimens are morphologically distinguishable from most specimens from other parts of the central and western Pacific, the Hawaiian populations may validly be accorded subspecific rank and termed *C. sponsalis nanus* Sowerby.

Tryon (1884: 24), who was also uncertain of the distinction between *C. sponsalis* and *C. ceylanensis*, considered *C. nanus* a variety of the latter in his arrangement but considered the possibility that both were varieties of *C. sponsalis*. Ostergaard (1935) also listed "*Conus ceylonensis sponsalis*," under which he stated, "I believe that this shell intergrades with *C. ceylonensis* Hwass and should therefore be termed a variety of that species, as Tryon places it."

Although the identity of *C. ceylanensis* remains problematical, the present writer is inclined to agree that it is probably conspecific with *C. sponsalis*. In this case, the name *sponsalis* has page priority, and there seems no reason why it should not take precedence over *ceylanensis*. It is hoped that collections in Ceylon and other Indian Ocean areas, to be made by the writer in the near future, will contribute towards a more definitive solution to this question.

C. sponsalis is one of the most abundant species of *Conus* on intertidal benches in Hawaii. Pleistocene fossils are known from Oahu (Ostergaard, 1928) and Molokai (Ostergaard, 1939).

Conus striatus Linné

Fig. 5 in Plate 1

Conus striatus Linné, 1758, Syst. Nat., ed. 10, p. 716.

Cucullus striatus (Gmelin). Röding, 1798, Mus. Boltenianum, p. 50.

Conus striatus Lamarck. Quoy and Gaimard, 1834, Voy. Astrolabe Zool., 3: 89, pl. 52, figs. 10, 10[1].

Leptoconus striatus (Linné). Adams and Adams, 1853, Gen. Rec. Moll., 1: 254.

Tuliparia striata. Gray, 1857, Guide Moll. Brit. Mus., 1: 5.

Conus floridus Sowerby, 1858, Thes. Conchyl., 3: 47, frontispiece, fig. 558.

Chelyconus striatus (Linné). Frauenfeld, 1869, Verh. k.k. Zool.-Bot. Ges. Wien, 19: 863.

Conus tulipa Linné var. *floridus* Sowerby. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 284.

Phasmoconus striatus (Linné). Cotton, 1945, Rec. South Austral. Mus., 8: 260.

Dendroconus striatus (Linné). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 292.

DESCRIPTION: Shell large, rather thin, elongate-ovate, the maximum diameter not at the shoulder but about one fifth of the distance from shoulder to base. Body whorl with fine, closely spaced transverse striae; aperture broad, flaring gradually toward the base. Shoulder angular, smooth. Spire striate,

canaliculate, usually concave, often extremely so and depressed below the shoulder, a peculiarity not typically found in specimens from other areas. Ground color pinkish white, irregularly clouded with blotches of brown or purplish brown composed of closely spaced transverse lines. Spire tesselated with brown and white. Interior of aperture white. Periostracum thin, yellow, translucent. In life, foot, siphon and rostrum tan mottled with brown.

LENGTH: Usually to 110 mm. A specimen measuring 120 × 53 mm. is in the collection of C. S. Weaver.

TYPE LOCALITY: "Hitoe."

REMARKS: Specimens from the Hawaiian Islands are characterized by having the spire depressed often to such an extent that the apex does not extend beyond the shoulder of the body whorl. In juvenile specimens, the spire is elevated and the sides of the aperture almost parallel.

C. striatus occurs uncommonly on Hawaiian reefs. It is typically found associated with a sand substratum. Pleistocene fossils of *C. striatus* have been collected by the author on Oahu.

Conus suturatus Reeve

Figs. 24–28 in Plate 2

Conus suturatus Reeve, 1844, Conch, Icon., 1: pl. 45, sp. 250; suppl. pl. 3, fig. 250b.

Dendroconus suturatus (Reeve). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.

Conus turbinatus Sowerby, 1858, Thes. Conchyl., 3: 25, pl. 10, fig. 227.

Lithoconus hawaiensis Bartsch and Rehder. Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 6.

DESCRIPTION: Shell solid; body whorl obsoletely striate toward the shoulder, the striae more pronounced, impressed but with an adjacent ridge, widely spaced toward the base. In young specimens, the striae are more pronounced over the entire body whorl. Aperture narrow, sides parallel. Shoulder angular, smooth; spire elevated in younger specimens, less so in larger ones, deeply striate, characterized by a ridge on each whorl at the junction of the preceding whorl. Ground color white, with broad transverse bands of orange brown (in smaller specimens) or orange pink (in larger specimens) on the body whorl. Base stained with pale orange brown or pale rose. Interior of aperture white. In smaller specimens, narrow bands of orange brown rectangles encircle the body whorl. Spire maculated with orange brown and white. Periostracum smooth, dark brown, opaque.

Most specimens from Hawaii are characterized by having the spire more elevated than those of the shells described and figured by Reeve.

LENGTH: To 50 mm.

TYPE LOCALITY: Port Essington, Australia.

REMARKS: *C. suturatus* is very closely related to *C. tessulatus*. In the latter, the rows of square or quadrangular blotches persist in adult specimens and vary from orange brown to, more usually, pink. In *C. suturatus*, this pattern is present in young specimens but is gradually superseded by the broad solid orange pink transverse bands mentioned in the description, and the transverse rows of rectangles are usually lost, as the shell grows larger. Some specimens of the two species may be virtually indistinguishable. In young *C. suturatus*, the broad transverse bands typically underly the juvenile pattern, the entire body whorl is usually striate, and the basal striae are accompanied by an adjacent ridge. In young *C. tessulatus* all areas between the rectangular blotches are typically white, impressed spiral striae occur only basally, and the areas between the striae are typically flat. The upper portion of the shell is smooth. Older, larger specimens of these two species are usually distinguishable by differences in color pattern cited in the accompanying descriptions.

C. suturatus is not common in shallow water in Hawaii, but many specimens have been

dredged in 4–50 fathoms off the major islands.

C. ambiguus Reeve (1844, Conch. Icon., 1: pl. 44, sp. 244) appears to be extremely similar and possibly identical. Some specimens collected in Hawaii have been labeled *C. ambiguus*. A definitive statement concerning *C. ambiguus* will not be made here, pending study of type material.

Conus tessulatus Born

Fig. 22 in Plate 2

Conus tessulatus Born, 1778, Ind. Rer. Nat. Mus. Caes. Vind., p. 131.
Conus virgo var. γ Gmelin, 1791, Syst. Nat., ed. 13, p. 3376.
Conus tessellatus Born. Bruguière, 1792, Enc. Meth. Vers, 1: 641.
Cucullus pavimentum Röding, 1798, Mus. Boltenianum, p. 41.
Conus tessellatus Lamarck. Menke, 1828, Synopsis Methodica Molluscorum, p. 45.
Conus tesselatus Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 173.
Conus desselatus Lamarck. Reichenbach, 1842, Land.-, Süssw.- u. See-Conch., p. 51, pl. 17, figs. 376, 377.
Conus tessellatus Bruguière. Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 17, fig. 1, p. 68.
Dendroconus tessellatus (Born). Adams and Adams, 1853, Gen. Rec. Moll., 1: 250.
Conus tessalatus Born. Theobald, 1860, Catal. Rec. Sh. Mus. Asiat. Soc. Bengal, p. 24.
Conus tesselatus Born. Weinkauff, 1874, Jahrb. Deutsch. Malak. Ges., 1: 245.
Conus tesselatus Bruguière. G. R. Batalha, 1878, Catal. Coll. F. R. Batalha, p. 25.
Conus tessellatus Hwass. Dautzenberg, 1893, Bull. Soc. Zool. France, 18: 80.
Conus edaphus Dall, 1910, Proc. U. S. Natl. Mus., 38: 223.
Conus tessullatus Born. Hirase, 1954, Illus. Handbk. Shells, p. 88, pl. 113, fig. 17.
Lithoconus tessulatus (Born). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 5, fig. 11.

DESCRIPTION: Shell fairly thick and stout. Body whorl smooth near the shoulder, bearing rather widely spaced impressed striae basally; base grooved; aperture narrow, the sides parallel; outer lip thin. Shoulder smooth, angular; spire concave, deeply striate, characterized by a ridge on each whorl at the junction of the preceding whorl; apex pointed. Ground color white, body whorl encircled by rows of quadrangular pinkish orange spots, usually crowded to form two transverse bands. Base characteristically stained with violet. Spire tesselated with pink and white. Interior of aperture white, violet at the base. In life, "yellowish white, foot mottled with brownish buff, anteriorly spotted with black; creeping disk buff yellow with darker veins; siphon creamy yellow tinged with brown, edged with yellow, with a transverse black spot at the anterior end" (Garrett, 1878).

LENGTH: 35–40 mm.

TYPE LOCALITY: Africa.

REMARKS: This species is extremely rare in shallow water in the Hawaiian Islands although it is widely distributed throughout the Indo-West Pacific region and reaches the west coast of Mexico (Hanna and Strong, 1949). Only one specimen collected alive in the Hawaiian Islands is known with certainty to the writer. It was collected by S. Sato in Haleiwa Bay, Oahu, depth 25 feet, and is in the Children's Museum of Honolulu, on loan from Mrs. Jean Bromley.

C. tessulatus was recorded from Hawaii by Garrett (1878). Dautzenberg (1937: 244) states that it was also recorded from Hawaii by P. Fischer, but no further reference is given. Three specimens in the U. S. National Museum, collected by the U. S. Exploring Expedition, are labeled "Sandwich Is." (and are shown in Plate 2, Fig. 22), but this locality datum is not to be considered reliable (J. P. E. Morrison, verbal communication).

Conus textile Linné

Fig. 2 in Plate 1

Conus textile Linné, 1758, Syst. Nat., ed. 10, p. 717.

Conus undulatus Solander *in* Cat. Portland Mus., 1786, p. 180, no. 3866.
Conus archiepiscopus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 747, pl. 345, fig. 5; pl. 346, figs. 1, 7.
Cucullus auriger Röding, 1798, Mus. Boltenianum, p. 49.
Cucullus gloria-maris Röding, 1798, Mus. Boltenianum, p. 49. (non *Conus gloria-maris* Chemnitz, 1777.)
Cucullus textile (Gmelin). Röding, 1798, Mus. Boltenianum, p. 50.
Conus panniculus Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 435.
Cylinder textile (Linné). Montfort, 1810, Conchyliogie Systematique, 2: 391.
(?) *Conus pyramidalis* Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 438.
Conus gloria-maris Perry, 1811, Conchology, pl. 25, no. 5. (non *gloria-maris* Chemnitz, 1777.)
Conus rete-aureum Perry, 1811, Conchology, pl. 25, no. 5.
Conus textiles Lamarck. Dufo, 1840, Ann. Sci. Nat., Ser. 2, 14: 177.
Conus textilis. Gray, 1842, Fig. Moll. Anim., pl. 10, fig. 1.
Conus victoriae Reeve, 1843, Conch. Icon., 1: pl. 37, figs. 202a, 202b.
Conus verriculum Reeve, 1843, Conch. Icon., 1: pl. 38, figs. 208a, 208b.
Conus concatenatus Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 110, fig. 1, p. 362.
Conus telatus Reeve, 1848, Conch. Icon., 1: suppl. pl. 1, fig. 270.
Conus scriptus Sowerby, 1858, Thes. Conchyl., 3: 41, pl. 23, fig. 563.
Conus tigrinus Sowerby, 1858, Thes. Conchyl., 3: 41, pl. 23, fig. 569.
(?) *Conus condensus* Sowerby, 1866, Thes. Conchyl., 3: 326, pl. 26, fig. 622.
Conus paniculus Lamarck. Paetel, 1873, Catal. Conch.-Samml. Paetel, p. 51.
Cylindrus textile (Linné). Morelet, 1889, Jour. Conchyl., 37: 133.
Darioconus textile (Linné). Cotton, 1945, Rec. South Austral. Mus., 8: 257.
Darioconus textilis (Linné). Kuroda, 1955, Venus: Jap. Jour. Mal., 18: 291.

DESCRIPTION: Shell large, ventricose, rather thin, subcylindrical-ovate. Maximum diameter of about one half shell length is reached about one fifth of the distance from shoulder to base. Body whorl transversely striate, the striae fine and closely spaced; aperture broad, flaring basally. Shoulder smooth; spire elevated, concave, acuminate, striate. Ground color white, with undulating longitudinal brown lines, interrupted by white triangles arranged as scales, and broad orange brown maculations disposed to form two or three interrupted transverse bands on the body whorl; the maculations streaked longitudinally with waved darker brown lines. Spire similarly marked. Interior of aperture white. Periostracum thin, yellow, translucent. In life, foot mottled brown on white. Tip of siphon reddish orange, followed proximally by bands of white and black; remainder of siphon white with closely spaced narrow brown bands.

LENGTH: To 100 mm.

TYPE LOCALITY: Banda Islands.

REMARKS: *C. textile* is rare in Hawaiian waters. It is found occasionally on reef platforms and to depths of at least 12 fathoms.

Conus vexillum Gmelin

Fig. 11 in Plate 1

Conus vexillum Gmelin, 1791, Syst. Nat., ed. 13, p. 3397.
(?) *Conus sumatrensis* Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 655, pl. 327, fig. 8.
Cucullus canonicus Röding, 1798, Mus. Boltenianum, p. 43. (non *Conus canonicus* Hwass *in* Bruguière, 1792.)
Conus vexillum Linné. De Fremery, 1802, Mus. Meyer., p. 82. (Not seen.)
Conus vexillum Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 268.
(?) *Conus leopardus* Dillwyn, 1817, Descr. Cat. Rec. Shells, 1: 364. (non *leopardus* Röding, 1798.)

Conus sulphuratus Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 66, fig. 3; pl. 78, fig. 4; p. 130.

Leptoconus vexillum. Adams and Adams, 1853, Gen. Rec. Moll., 1: 252.

Conus planorbis Born. Oostingh, 1928, Misc. Zool. Sumatrana, no. 28: 4. (error. Fide Misc. Zool. Sum., no. 49: 6.)

Rhizoconus vexillum (Gmelin). Cotton, 1945, Rec. South Austral. Mus., 8: 251.

DESCRIPTION: Shell large, rather thin. Body whorl obsoletely striate; aperture rather broad, sides parallel. Shoulder broad, angular, smooth. Spire moderately elevated, obtuse, somewhat canaliculate, striate. Color of body whorl white, broadly banded with yellowish brown, stained with darker brown at the base, with irregular chocolate longitudinal waved lines which often branch and are partially interrupted to form a white band at the middle and another at the shoulder. Spire white with yellow apex and broad radiating chocolate bands, some of which are continuous on the body whorl. Interior of aperture white. Periostracum dark green, thick, opaque; ridged. In life, foot and siphon greenish black.

LENGTH: To 135 mm.

TYPE LOCALITY: None.

REMARKS: Although this species was first reported from Hawaii as *C. vexillum* (Garrett, 1878), it has generally been known in Hawaii as *C. sumatrensis*. Examination of specimens in the U. S. National Museum and in collections made by the author in Micronesia as well as Hawaii revealed morphological overlap and intergrades between typical specimens of both species. Further confusion is found in the literature. Kiener (1847: 81) stated under *C. sumatrensis*, "Coquille qui par sa forme se rapproche de la précédente [*C. vexillum*]; elle est reconnaisable surtout par ses lignes longitudinales ramifées." Tryon (1884: 39) stated, on the other hand, under *C. vexillum*, "Spire often variegated with white and chestnut broad flames, the latter often overlaying also the lighter chestnut of the body whorl." Most authorities have considered the two as distinct species. The figures given in Reeve (1843: pls. 1 and 3) show extreme variants, while the specimens figured by Sowerby (1857: pl. 7) are hardly distinguishable.

C. vexillum is a relatively uncommon species on Hawaiian reefs. It is known to occur to a depth of 25 fathoms. Pleistocene fossils are known from Molokai (Ostergaard, 1939, as *C. sumatrensis*).

Conus vitulinus Hwass *in* Bruguière

Fig. 14 in Plate 1

Conus vitulinus Hwass *in* Bruguière, 1792, Enc. Meth. Vers, 1: 648, pl. 326, fig. 3.

Conus vitulinus Bruguière. Lamarck, 1810, Ann. Mus. Hist. Nat. Paris, 15: 265.

Conus vulpinus Schubert and Wagner, 1829, Syst. Conch. Cab., 12: 56, pl. 222, fig. 3073. (non *vulpinus* Hwass *in* Bruguière, 1792.)

Conus vulpinus Wagner var. A. Küster, 1837–1840, Syst. Conch. Cab., ed. 2, 4: 29, pl. 3, fig. 7. (non *vulpinus* Hwass *in* Bruguière, 1792.)

Conus planorbis var. *vitulinus* Hwass. Mörch, 1852, Catal. Conchyl. Yoldi, p. 69.

Dauciconus vitulinus (Bruguière). Cotton, 1945, Rec. South Austral. Mus., 8: 246.

Leptoconus vitulinus (Bruguière). Kira, 1955, Coloured Illus. Shells Japan, p. 36.

Lithoconus vitulinus (Hwass). Kaicher, 1956, Indo-Pacific Sea Shells, Sect. 5, pl. 2, no. 7a.

DESCRIPTION: Shell thick and solid. Body whorl obscurely striate near the shoulder, the striae becoming more pronounced and granular basally. Aperture narrow, the sides parallel. Shoulder angular, smooth; spire depressed, slightly canaliculate, striate. Color of body whorl usually deep reddish or purplish brown, darker at the base, with white bands mottled with ground color at the shoulder and below the center; the bands contain one to several rows of brown dots. In large specimens, the reddish brown areas often interrupted by longitudinal white blotches. Spire arcuately tesselated with brown and white. Perios-

tracum gray, thick, opaque, closely striate transversely. In life, visible portions of foot and siphon bright lemon yellow.

LENGTH: 70 mm.

TYPE LOCALITY: Indian Ocean.

REMARKS: Small specimens of this species closely resemble *C. litoglyphus*. *C. vitulinus* may be distinguished by having striae above the central band, rows of brown dots on the white bands, and absence of a pointed apex.

C. vitulinus is a relatively uncommon species on Hawaiian reefs. It is known to occur to a depth of 30 fathoms. Pleistocene fossils are known from Molokai (Ostergaard, 1939).

A single specimen labeled *Conus planorbis* Born in the collection of the B. P. Bishop Museum (No. 68990) was dredged in Honolulu Harbor. The Museum of Comparative Zoology contains another specimen (No. 146332) collected at Midway Island by J. Chalean, apparently alive when collected. These specimens are extremely similar to, and may be synonymous with, *C. vitulinus*, as has been suggested by some workers (p. 395).

POSSIBLE ADDITIONAL VALID SPECIES IN HAWAII

Conus elisae Kiener

Fig. 4

Conus elisae Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 64, figs. 1, 1a, p. 341.

(?) *Conus stellatus* Kiener, 1845, Spéc. Gén. Icon. Coq. Viv., 2: pl. 99, fig. 3, p. 225.

DESCRIPTION: Shell subcylindrical; maximum diameter slightly more than one half the length. Body whorl obsoletely striate, the striae slightly more pronounced and as raised ridges toward the base. Aperture rather broad, flaring slightly basally. Shoulder smooth, rounded. Spire moderately elevated, obtuse, straight or slightly convex, obsoletely striate. Color dark reddish brown, as many closely spaced and intersecting longitudinal lines separated by small white spots; occasionally with larger white subtrigonal blotches as in *C. pennaceus;* two broad transverse bands either side of the center appear to be superimposed on this pattern. These bands are more solidly colored and are similar to the reddish brown areas of *C. pennaceus* in that they bear narrow transverse closely spaced lines finely dotted with white. Color pattern of the spire similar to that of the bands on the body whorl. Interior of aperture bluish white.

FIG. 4. "*Conus elisae* Kiener," 35 × 19 mm. Specimen collected by C. E. Cutress on Rabbit Island, off Oahu. Photograph by C. E. Cutress.

LENGTH: Specimens in the U. S. National Museum and Academy of Natural Sciences of Philadelphia range from 15.5 mm. to 27 mm. in shell length. The specimen illustrated in Figure 3 measures 35 × 19 mm.

TYPE LOCALITY: None.

REMARKS: *Conus elisae* was first reported from Hawaii by Weinkauff (1874). Recently, a number of specimens agreeing with the description and figure of this species have been collected on the islands of Kauai and Niihau. Sowerby (1858: 43) considered this species to be synonymous with *C. pennaceus*, a conclusion with which the present writer has been inclined to agree. However, no specimens intermediate in character between

Kiener's *C. elisae* and typical *C. pennaceus* have been found, despite an increasing number of specimens collected during the past year. Moreover, the microhabitat of the Hawaiian specimens referred to seems to differ from that of typical *C. pennaceus*. The former are typically found buried as deep as six inches under sand (A. H. Cornelison, verbal communication) while the latter are typically found on or partly buried in sand under rocks (Kohn, 1959). It seems reasonable at the present time to consider *C. elisae* as a possibly valid species. The problem requires further investigation.

UNIQUE RECORD FROM HAWAII

Conus smirna Bartsch and Rehder

Fig. 13 in Plate 1

This species is known only from a single specimen, the type, described by Bartsch and Rehder (1943). It was dredged near Lanai ("Ranai") in 257–312 fathoms by the U. S. Fisheries steamer "Albatross."

SPECIES KNOWN IN HAWAII ONLY FROM COLLECTION OF DEAD SPECIMENS

To the author's knowledge, there are no records of living specimens of the following species from the Hawaiian archipelago.

Conus aulicus Linné

C. auratus is probably a synonym of *C. aulicus*.

Ostergaard (1928) listed *C. auratus* as occurring in the fossil state on Oahu. The present writer is quite convinced that the species referred to was *C. pennaceus*, since Ostergaard (1928) also mentions the normal habitat of living specimens. However, at least one fossil specimen of *C. aulicus* is known from Oahu. It was collected about five feet above high tide mark near Nanakuli by E. C. Jones in March, 1954. It is at present in the collection of the Children's Museum of Honolulu (No. 2747).

Specimens now considered to be narrow-shelled variants of *C. pennaceus* because of the abundance of intergrades were listed as *C. auratus* by Edmondson (1933). Edmondson (1946) cited both *C. auratus* and *C. omaria*. The same figure of a rather typical shell of *C. pennaceus* was labelled *C. auratus* by Edmondson (1933) and "*Conus omaria* (?)" in the 1946 edition.

Specimens of *C. aulicus* were collected by the Tanager Expedition at Kure (Ocean) Island and Pearl and Hermes Reef and are in the collection of the B. P. Bishop Museum (Nos. 66438, 66439, 66205). A shell from Midway Island which is quite fresh in appearance but was empty when collected is in the collection of C. A. Allen.

Conus aureus Hwass *in* Bruguière

A number of well-preserved shells of this species have been collected on beaches along the windward coast of Oahu.

Conus auricomus Hwass *in* Bruguière

This species has been known erroneously as *C. clavus* Linné (see Dodge, 1953). Several specimens have been collected from dredged material at Honolulu, Oahu, and at Midway Island. *C. magnificus* Reeve, recorded by Garrett (1878) from the Hawaiian Islands, is probably synonymous. A label, "*Conus magnificus* Reeve. Hawaiian Ids.," is present in the Garrett collection in the B. P. Bishop Museum, but no shell is present.

Conus cylindraceus Broderip and Sowerby

Several shells have been collected from dredged material at Midway Island. No specimens are known from the main Hawaiian Islands (Thaanum, *in litt.*).

Conus fabula Sowerby
(=**Conus scabriusculus** Dillwyn?)

The only known specimen, probably a subfossil, was collected at Makua, Oahu, by W. C. Ross.

Conus tenuistriatus Sowerby

Some authors have considered this species synonymous with (Tryon, 1884) or a variety of (Couturier, 1907; Dautzenberg, 1933) *Conus glans* Hwass *in* Bruguière. Several dead specimens have been dredged and a few have been collected on beaches in the Hawaiian Islands.

Conus tulipa Linné

Ostergaard (1928) reported collection of several fossil specimens, one of which is figured, of *Conus tulipa*. The identification of a fossil specimen, presumably collected by Ostergaard, in the Hawaii Marine Laboratory reference collection, has been verified by the writer as *C. tulipa*. Ostergaard (1928) referred to a "live immature specimen" of *C. tulipa* collected in Hawaii by C. H. Edmondson. It is possible that the specimen referred to was a *C. obscurus*, as several older specimens of that species were labeled *C. tulipa*. However, a single juvenile specimen of *C. tulipa* (No. 20), collected at Waikiki Reef, Oahu, is in the Hawaii Marine Laboratory reference collection. It is not known whether or not this specimen was alive when collected, but it is in fresh condition. A number of shell fragments of *C. tulipa* have also been collected on Hawaiian beaches.

UNVERIFIED AND INACCURATE RECORDS FROM THE HAWAIIAN ISLANDS

Conus arenatus Hwass *in* Bruguière

A single beach specimen, labeled "Hawaii. coll. W. H. Pease," is in the U. S. National Museum (No. 5038). No other specimens are known from the Hawaiian Islands, and the record may be in error as to locality.

Conus aristophanes Sowerby

This species, considered by Tomlin (1937) and others as synonymous with *C. coronatus* Gmelin, was described by Sowerby (1858) from the Philippine and Hawaiian islands. The latter locality is almost certainly in error.

Conus atramentosus Reeve

This is the type species of the genus *Lovellona* of Iredale (1917). Thiele (1931) considers *Lovellona* a section of the genus *Mitromorpha* A. Adams (1865) and places it in the subfamily Cytharinae of the family Conidae. Other authorities place *Mitromorpha* in the family Pleurotomidae (Simroth, 1896–1907).

Conus cancellatus Hwass *in* Bruguière

The type locality of this species is given in Bruguière (1792: 713) as "l'isle d'Owhyhée dans l'ocean pacifique." This is presumably an error, since no specimens from the Hawaiian Islands are known to the writer, although there is some resemblance to *C. acutangulus*. *C. cancellatus* is found in Japan.

Conus emaciatus Reeve

This species, considered by Tomlin (1937) and others as a juvenile of *C. virgo* Linné, was reported from the Hawaiian Islands by Sowerby (1858: pl. 12, sp. 191). This reference may be in error, since no specimens from Hawaii are known to the writer or D. Thaanum (*in litt.*).

Conus fusiformis Pease

Pease (1860) described this species from the Hawaiian Islands. It belongs to the genus *Mitromorpha*. (See under *C. atramentosus*.)

Conus miliaris Hwass *in* Bruguière

A specimen in the U. S. National Museum (No. 338481) now labeled "*Conus miliaris* Hwass" was collected by D. Thaanum at Keaukaha, near Hilo, Hawaii. Three live specimens were found in a sand pocket in the reef and apparently none have been collected since (Thaanum, *in litt.*). The specimens were first labeled by W. H. Dall as a variety of *C. abbreviatus*. The single discovery of three individuals in a small area suggests a small, isolated, aberrant population with possible fixation of atypical morphological character-

istics by genetic drift. The circumstances of collection thus lend support to Dall's conclusion that the specimens represent a variant of *C. abbreviatus*. However, the specimens agree quite completely on morphological grounds with typical *C. miliaris*, which is otherwise not known to occur in the Hawaiian Islands. It is possible that the specimens under consideration may have hatched elsewhere and have been carried ashore on Hawaii by currents during the pelagic larval stage. In either event, the population has apparently not become established in Hawaii.

The Museum National d'Histoire Naturelle, Paris, contains two additional specimens labeled "Kauai (Sandwich) Rémy 1857."

Conus parvus Pease

Pease (1868) having discovered that *C. fusiformis* was preoccupied, renamed that species *C. parvus*. See under *C. fusiformis*.

Conus virgo Linné

Although Garrett (1878) reported this species from the Hawaiian Islands, there is no specimen in the Garrett collection in the B. P. Bishop Museum, and no other records are known to the writer. Demond (1957) also lists this species from Hawaii.

SUMMARY

The gastropod genus *Conus* is represented by 33 species in the Hawaiian archipelago. This number comprises only species of which more than one individual has been collected alive in the area between Kure (Ocean) Island and the island of Hawaii. Synonymies, descriptions, type localities, and notes are given for each of these species.

One possibly additional valid species, a unique record of one species, seven species known in Hawaii only from the collection of dead specimens, and unverified and inaccurate records of nine species from the Hawaiian Islands, are cited.

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Why some strains of Lyngbya majuscula are toxic, and others are not, is still mysterious

A Dermatitis-Producing Alga in Hawaii

Preliminary Report

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LYNGBYA MAJUSCULA Gomont is a nominal blue-green alga, a member of the plant phylum Cyanophyta; its color, however, is usually an olive drab. It grows in the form of long, unbranched hair-like filaments, one cell in diameter. The filaments, without holdfasts, become entangled in other algae, coral, or even sand; and as the cells proliferate, the strands become longer. With strong waves the massed filaments are broken away and carried to become caught on other objects or to be thrown on the shore by the waves. When growing on the bottom or cast up on the shore, the alga usually occurs in characteristic masses like mats of felted hair.

DR. BANNER

Increasing Prevalence

The species is widespread throughout the tropical Pacific and Indian Oceans, occurring often in great abundance from the intertidal zone to a depth of about 100 feet. The first record of it from Hawaii was made in 1912, so presumably it is part of the native flora. However, both by accounts of old fishermen and by observations of trained algologists, it was less abundant before World War II than it is at present; what factors have contributed to its increase are not known.

L. majuscula has never before been reported to cause dermatitis, although it has been reported to have caused deaths of horses feeding on it on beaches of Ceylon. In Hawaii some bathers, and fishermen in whose nets the weed became entangled, have been aware for years that it would cause irritation of the skin, but this property of the seaweed was not called to the attention of local medical workers until the summer of 1958 when large concentrations of a toxic strain were found at Kailua, Oahu.

During the summer of 1958 Dr. George Chu of the University of Hawaii, Dr. Harry L. Arnold, Jr. of Straub Clinic, and Col. Franklin Grauer of Tripler Hospital initiated investigations on the relationship between the alga and dermatitis; their preliminary findings they reported to the Hawaiian Academy of Science. In the spring of 1959 a small investigation was started at the Hawaii Marine Laboratory with a grant from the Honolulu Chamber of Commerce. Personnel working on the problem included Dr. Philip Helfrich, Mr. Robert Morris, Miss Angeline Silva and myself.

Tests for Toxicity

The original test for toxicity in the alga was a patch test on humans, as is reported by Col. Grauer in the accompanying article. In the studies at the Hawaii Marine Laboratory we found the same results could be obtained if the alga were stored in a frozen condition dried by hot air. However, because of the discomfort of the skin tests to the investigator, and because of the possible danger of repetitive tests on the same individual, we have attempted to develop a more objective and less ob-

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jectionable form of assay. Patch tests on experimental animals were unsatisfactory because of the difficulty in keeping the patches intact. Voluntary feeding tests on white mice showed some promise, especially where the dried alga was combined with standard mouse food in pellets. When the mouse ate enough of the test meal, it would develop conjunctivitis, become lethargic, and die within two days. However, as even starving mice did not eat much of the pellet containing toxic Lyngbya and would scatter fragments of the pellet, giving us no control of the amount of alga fed, the test was discarded. Two other tests were found to be satisfactory. In one the ground and dried alga was suspended in a fluid gelatin solution to prevent settling and force fed to mice; with a feeding of 0.3 percent to 1.0 percent body weight the mouse would develop muscular weakness, convulsions, and die within two to three hours with reactions proportional to the toxicity of the sample and the amount fed. In the other test dried alga was extracted with either ethanol or water, the solution diluted with normal saline and injected intracutaneously into rabbits or guinea pigs in amounts equivalent to 0.5 to 0.02 mg of the dried alga. The resulting swelling and erythema was proportional to the toxicity of the sample and its dilution. The results of both tests were found to parallel the results of patch tests on humans. In both tests it was found that if the material fed or injected be concentrated enough, toxic reactions would be obtained in strains not causing human reaction. This appears to indicate that the strains not producing human dermatitis may actually have the toxin in low concentrations.

Toxic Strains in Few Places

In the surveys conducted about Oahu, Molokai, and Kauai it was found that L. majuscula was common on numerous beaches. However, either by human patch test or by guinea pig injections, toxic strains were found only in a few localities. Strongly toxic algae were found in about 80 feet of water off Waikiki and at Laie on the island of Oahu, and at Hanalei on Kauai, while moderately toxic algae were found at Waimanalo, Kailua, Kaaawa, and Makaha on Oahu and at Pilaau on Molokai. In other areas, while the alga might occur in moderate to great abundance, as in Kaneohe and Hanauma Bays, no toxic strains were found.

It is notable that the deep form collected off Waikiki and one small mass of alga collected in Kaneohe Bay, both giving positive reactions in tests, were of red rather than the usual olive drab color. There was no morphological differentiation between the two strains and such a change of color is well-known in the blue-green algae where the normal blue-green pigment, phycocyanin, is reduced to a red pigment, phycoerythrin, under conditions of decreased oxygen tension. There are no differences between the toxic and nontoxic strains of the algae that are considered important enough for a systematic separation into different species.

Relation to Fish Poisoning?

A number of workers have suggested the Ciguatera type of toxicity of fishes—the paralytic toxin that renders certain of the normally desirable species of ground fish, like red snappers, dangerous to eat in limited areas of the tropics—may stem from blue-green algae at the base of the food chain, and some have suggested Lyngbya majuscula, in particular, as the alga that causes the toxicity. In addition, local fishermen from Molokai and Kauai have suggested that Hawaiian mullet poisoning—an intoxication in which the flesh, and especially the head of mullet and surmullet ("nightmare weke"), causes hallucinations and nightmares—is the result of the fish eating this alga. In the current studies no indications have been found of either of these relationships.

Ciguatera and Lyngbya toxins appear to have different solubilities, with that of Lyngbya soluble in water and in alcohol, and that of Ciguatera soluble in alcohol and some of the fat solvents; moreover, the symptoms on feeding to test animals is quite different. It has not been possible to obtain any of the toxic Hawaiian fish for study, but on the basis of the distribution of the toxic strains of the alga and the toxic strains of the fish no relationship is indicated, for the areas where the fish are reputedly the worst do not have highly toxic alga, and where the alga is the worst, the fish are innocuous. However, as our studies are in their initial phases, no positive statements as to possible relationships can be made.

Summario in Interlingua

Lyngbya majuscula es un alga filamentose de color blau-verde que es extensemente distribuite in le tropic Oceanos Pacific e Indian e que es cognoscite in Hawai depost 1912. Ben que illo es commun in multe plagias de Hawai, il es solmente in alicun plagias al latere del vento del insula Oahu que illo ha manifestate intense toxicitate pro le pelle human durante le estates de 1958 e 1959. Solmente casos sporadic de tal toxicitate habeva essite notate in previe annos. Extractos alcoholic del alga es toxic pro le pelle human e etiam post injection in animales. Le substantia molite del alga es toxic post administration oral a muses. Un relation con invenenamento de pisce es considerate como possibile.